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Spectacles and Silver Ys: a synthesis of the systematics, cladistics and biology of the Plusiinae (Lepidoptera: Noctuidae)

Ian J. Kitching

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Synopsis

A comprehensive historical review of the higher classification of the Plusiinae is presented, with particular reference to the different generic concepts and interrelationships that have been proposed. The position of

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the subfamily within the Noctuidae is considered separately. A cladistic analysis of 47 generic-level taxa of plusiines and 11 outgroups was performed, using the type species of each as an exemplar. A total of 216 characters is described, drawn from the morphology of the head, prothorax, vestiture, wings, legs, abdomen and male and female genitalia. These data were analysed using the numerical cladistic program PAUP and at least 50 equally-parsimonious cladograms of 648 steps were generated. The character state changes supporting the various alternative subtopologies are discussed and a preferred 648-step cladogram constructed. A further analysis revealed the existence of 16 647-step cladograms but, after character analysis, these were all rejected. The preferred 648-step cladogram is evaluated, first in terms of characters, and then in terms of its constituent clades. Under each of the genera in the latter section, a brief review of biology, distribution and other points of interest is also included. This assessment allowed characters of low reliability to be identified and subsequently eliminated from the data. The reduced data set, less the outgroups, was analysed once more using PAUP. At least 50 equally-parsimonious cladograms were again found. A manual strict consensus cladogram analysis was then performed using these cladograms and, from the results, a consensus classification of the Plusiinae constructed, using the conventions for annotated Linnaean hierarchies. Four tribes are recognized in the Plusiinae: the Omorphinini, Abrostolini, Argyrogrammatini and Plusiini. The last is divided into three subtribes: the Euchalciina, Autoplusiina and Plusiina. Several genera (*Shensiplusia, Pseudochalcia, Diachrysia, Anagrapha, Rachiplusia, Loboplusia* and *Erythroplusia*) cannot be placed with confidence and are included *incertae sedis* in the classification. *Cornutiplusia, Lophoplusia, Ctenoplusia* and *Thysanoplusia* are recognized as good genera, although with reservations regarding the last of these. *Pseudoplusia, Eutheiaplusia, Acanthoplusia, Adeva* and *Caloplusia* are interpreted as subgenera of *Chrysodeixis, Plusiotricha, Ctenoplusia, Euchalcia* and *Syngrapha* respectively. This classification is compared with the five recent higher classifications proposed for the Plusiinae. Finally, the larval foodplant associations and biogeography of the subfamily are briefly discussed. One new subtribe is erected and five new combinations made. One species and one generic synonymy are proposed. Four previously synonymized genera are recognized as valid while a further five genera are reduced to subgeneric status.

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Introduction

For over 80 years, the higher classification of the family Noctuidae has consisted of a non-hierarchical series of largely artificial subfamilies, based upon a small number of simple and readily observable characters. There have been frequent small adjustments to the positions of individual genera; more rarely a new tribe has been erected (although usually defined only for a regional fauna), and never has a whole subfamily been revised. However, if a useful and predictive higher classification of the noctuids is to be constructed, then problems have to be addressed at the tribal level and above.

Subsequent to my recent review of noctuid higher classification (Kitching, 1984), I decided to analyse the interrelationships of the genera of the subfamily Plusiinae, by the critical application of cladistic methodology. The plusiines were chosen for a number of reasons. First, and perhaps foremost, there were reasonable grounds for supposing that, even as currently constituted, the Plusiinae are a monophyletic group. Thus, it would be unlikely that any of the constituent genera would be overlooked by their being placed in other subfamilies. This supposition is strongly supported by the observation that, since Hampson's (1913) *Catalogue*, no pre-existing genera have been transferred into the Plusiinae from elsewhere in the Noctuidae. Additional genera have arisen either by the discovery of new species (e.g. *Loboplusia, Eutheiaplusia*) or by the subdivision of pre-existing plusiine genera. A few genera (e.g. *Phyprosopus* Grote, *Diloba*) have been transferred out of the Plusiinae. Second, the plusiines are a relatively small subfamily of around 400 species and 45 genera. They were thus more amenable to analysis within my terms of reference than, say, the more economically important but much larger Noctuinae (with

approximately 2000 species in 150 genera). This is not to say that the plusiines are merely of academic interest. The subfamily includes a number of major agricultural pests, notably *Trichoplusia ni, Pseudoplusia includens, Chrysodeixis* spp. and *Thysanoplusia orichalcea* (Fabricius). Thus, a predictive higher classification of the Plusiinae is vital for the effective applied entomology of the group. Finally, the collections of the British Museum (Natural History) (BMNH) contain specimens of about 80% of the world species and 96% of the genera of plusiines: relatively complete coverage by any standards.

It was impossible to conduct a species-level analysis of the subfamily and so some selection of taxa to be included had to be performed initially. I decided to concentrate on one species from each genus or genus-group taxon, choosing the type species for convenience. Characters were drawn primarily from the external morphology of the adult moths. Little consideration was taken of the internal morphology, and none of the immature stages or biology. A cladistic method was chosen primarily because of the explicit manner in which it handles characters and their state transformations. There is no excuse for hiding behind vague or authoritarian statements of relationships. I hope my reasoning on such issues as character coding, polarity and interpretation are clear: that of many previous authors has not been so.

The history of the subfamily Plusiinae

The higher classification of the plusiines

In the following historical review of the Plusiinae, several terminological conventions have been employed. Members of the subfamily in general are referred to as 'plusiines', while 'plusias' refers collectively to the tribes Argyrogrammatini and Plusiini (i.e. the Plusiinae less the Abrostolini and Omorphinini). The taxon names used are those employed in the publication being discussed at that point. Current nomenclature, where this differs, is given in square brackets. This approach was adopted to facilitate back-referencing by the reader and to clarify some of the earlier nomenclatural anarchy.

The emergence of the Plusiinae

Linnaeus (1758) described the first plusiine noctuids within the subsection of *Phalaena Noctua* characterized as 'spirilingues dorso cristato'. Of these, *triplasia* was well separated from the remaining five species (*chrysitis, gamma, interrogationis, jota* Linnaeus and *festucae*). This arrangement was followed by Denis & Schiffermüller (1775), who included *triplasia* (together with *asclepiadis* [Denis & Schiffermüller] and two other noctuids) in the informal group Y (Larvae Pseudogeometrae, Ph[alaenae] Noctuae Submetallicae), and the other plusiines in group Z (Larvae Semigeometrae, Ph[alaenae] Noctuae Metallicae). These groups were accepted by Borkhausen (1792) and formally named by Ochsenheimer (1816) as the genera *Abrostola* and *Plusia*. Haworth (1809), however, chose to treat *triplasia* and *asclepiadis* as a section of *Noctua* (19 Arctuo-strigatae) and included the other plusiines in the genus *Phytometra* (section Metallicae), a decision that was to have important repercussions subsequently.

Hübner [1821] increased the number of plusiine genera to ten. *Abrostola* was again placed in a separate 'family', while the remaining plusiine species were allocated to *Euchalcia, Agrapha, Syngrapha, Autographa, Polychrysia, Panchrysia, Diachrysia, Chrysaspidia* and *Chrysodeixis*. However, these genera were, by and large, ignored for the remainder of the nineteenth century.

The Plusiinae as a family-group entity originated as the Tribus Plusidi, including three genera: *Abrostola, Chrysoptera* [*Lamprotes*] and *Plusia* (Boisduval, 1828). Duponchel (1844) modified this arrangement by treating the latter two groups as 'subgenera' of *Plusia. Plusia* (s. str.) was further subdivided into three unnamed sections based on wing pattern. Guenée (1841; 1852–4) and Herrich-Schäffer (1845) proceeded along similar lines.

This bigeneric system persisted for many years (e.g. Grote, 1874; 1875; Hampson, 1893–5), although Smith (1882–3) united the two into a single genus *Plusia*. Gradually, however, opinion swung towards the view that the omnibus genus *Plusia* ought to be subdivided, given the structural diversity displayed by its included species. Both Grote (1882) and Tutt (1891–2)

considered *Deva* [*Pseudeva*] to be a good genus, and by 1875, Grote had accepted Hübner's [1821] generic groupings, to which he added *Chrysanympha*. Butler (1892) also argued for separate generic status for *Polychrysia* and considered *Deva* (sensu Grote and others) to be synonymous. *Polychrysia* thus included additional species currently referable to *Lamprotes* and *Pseudeva*.

On the basis of characters drawn from the wing-shape, labial palps and eyes, Dyar (1902) recognized seven genera of plusias: *Polychrysia, Panchrysia, Plusia, Autographa, Euchalcia, Syngrapha* and a new genus, *Eosphoropteryx*. This arrangement was endorsed, for the most part, by Ottolengui (1902) in a paper published in the same journal only a few pages *before* that of Dyar. Forbes (1914) reverted to the omnibus *Plusia* but included Dyar's subdivisions in a note.

Meanwhile, Hampson (1913) was subdividing the plusiines along completely different lines. The subfamily was renamed the Phytometrinae, with the type genus and species, *Phytometra festucae*. This change resulted from Hampson's criterion for type species designation. Irrespective of previous designations, Hampson chose as the type species of a genus, the *first* species included when that genus was described, unless otherwise explicitly specified by the author at the time (McDunnough, 1916). Thus, the type species of *Phytometra* Haworth was considered to be *festucae*, despite Westwood's (1840) designation of *aenea* ([Denis & Schiffermüller]) [= *viridaria* (Clerck)]. Thus *Plusia*, the type species of which was taken by Hampson to be *deaurata*, became a subjective synonym of *Phytometra*.

In addition to '*Phytometra*', fourteen other genera were placed in the 'Phytometrinae', on the basis that they were quadrifine noctuids with lashed eyes. In his 'phylogeny' of the subfamily, Hampson considered that the unknown ancestor had given rise to *Omorphina* (transferred to the Erastriinae by Kostrowicki, 1961; but see below), *Diloba* (of current uncertain position, but probably a noctuid), *Abrostola* and *Palaeoplusia*. *Mouralia* was derived from *Abrostola*, while *Palaeoplusia* was ancestral to '*Phytometra*'. This last genus contained by far the majority of the plusiines but from it arose five further genera: *Plusidia, Pseudeva, Eosphoropteryx, Chrysoptera* [*Lamprotes, Polychrysia*] and *Syngrapha*. *Plusiopalpa* was considered to be a derivative form of *Chrysoptera*, while, by additional tibial spination on the fore- and mid-legs and a reduction in the size of the eyes, *Autographa* (comprising only the present *Syngrapha parilis* (Hübner), another result of Hampson's type species designations), *Rachiplusia* and *Caloplusia* were derived from *Syngrapha*. *Syngrapha* itself was divided into two parts, corresponding approximately to the current genera *Syngrapha* and *Autoplusia*. In *Chrysoptera, sica* (Graeser) was distinguished from the remaining species by an excised forewing termen, while '*Phytometra*' was split into four groups, depending on whether the male antennae were bipectinate and apically ciliate ('*P.*' *pterylota*), bipectinate and apically serrate ('*P.*' *psectrocera* Hampson), serrate ('*P.*' *lavendula* (Hampson) and '*P.*' *gerda* (Püngerler)) or ciliate (the remaining 151 species). *Chrysanympha formosa* was placed in *Abrostola*.

Hampson's arrangement was followed in its entirety by the authors of 'Seitz': Warren (1913), Draudt (1940) and Gaede (1937–9). However, other workers were far from satisfied. McDunnough (1916) corrected many of Hampson's erroneous type species designations, including that of *Phytometra*. This allowed him to replace '*Phytometra*' with *Autographa*, return *parilis* to *Syngrapha* and to reinstate Plusiinae as the subfamily name. At this time, it should be noted, the type species of *Plusia* was considered to be *chrysitis* (Linnaeus), a point to which I shall return below.

McDunnough's revision of the Nearctic plusias

Barnes & McDunnough (1917) advocated a system that was something of a hybrid between those of Dyar (1902) and Hampson (1913), and which was largely accepted by McDunnough (1938) in his later checklist. However, shortly afterwards, McDunnough (1944) published a revision of the Nearctic plusias, which represented a significant departure from all previous classifications, and for the first time in plusiine systematics, genitalic characters were employed. The subfamily (less *Abrostola* and *Mouralia*) was split into three sections based on the form of

the clavus. Section A, in which the clavus was a short, slightly setose knob arising from a broad base, included *Syngrapha, Anagrapha* and *Caloplusia*, and was additionally characterized by 'readily recognizable' tibial spines. Section C comprised *Pseudeva* and *Adeva*, genera in which the clavus was not clearly defined, while section B, in which the clavus was a long, thin, variably setose rod, contained the balance of the species. This latter section comprised twelve genera: *Autoplusia, Trichoplusia, Argyrogramma, Pseudoplusia, Rachiplusia, Chrysaspidia [Plusia], Autographa, Chrysanympha, Eosphoropteryx, Polychrysia, Plusia [Diachrysia]* and *Agrapha [Allagrapha]. Palaeoplusia* was synonymized with *Chrysaspidia [Plusia]*.

By way of an aside, it was subsequently noted by Franclemont (1964) that Grote (1896) had designated *Phal[aena] Noct[ua] glauca* (Cramer) [= *ahenea* Hübner] as the type species of *Agrapha. Agrapha* originally contained two species, *aerea* and *glauca*, which Franclemont considered were not congeneric. Because he agreed with McDunnough that *aerea* represented a genus distinct from *Plusia [Diachrysia]* but that *Agrapha* was inappropriate, Franclemont proposed the genus *Allagrapha*, noting similarities in the male and female genitalia with *Macdunnoughia* that were not shared with *Plusia [Diachrysia]*.

Forbes (1954) followed McDunnough's (1944) subdivision of the plusiines but treated the latter's genera as subgenera of *Plusia*, as did Zimmerman (1958). Inoue & Sugi (1958) attempted to apply the new system to the Japanese fauna but the result was not very satisfactory; *Autographa*, in particular, became highly heterogeneous.

Meanwhile, the studies of Forbes (1910), Fracker (1915), Gerasimov (1935) and Hinton (1946), amongst others, were stimulating interest in the use of the detailed larval morphology in lepidopteran classification. Initially, largely due to lack of material, the results consisted mainly of descriptions (e.g. Gardner, 1941; 1947; 1948*a*) but soon sufficient taxa had been examined and described to allow some comparative work to be undertaken. Crumb (1934) split the plusiine larvae into two groups based on the ordination of the crotchets. Gardner (1948*a*) noted differences in chaetotaxy, skin ornamentation, proleg number, maxillary palp and antennal segment shape but made no subdivisions using these characters. A similar dichotomy in chaetotaxy was found by Timlin (1955) but unfortunately, like Gardner, the number of species examined was too small to be able to conclude anything definitive about the interrelationships of the genera.

This position was changed markedly by Crumb's (1956) study of the larvae of 25 species in 14 genera of Plusiinae. On the basis of characters drawn mainly from the mandibles and chaetotaxy, he grouped the plusiines into nine informal genera. Four of these (*Abrostola, Polychrysia, Chrysaspidia [Plusia]* and *Caloplusia*) corresponded to McDunnough's generic concepts. *Trichoplusia, Pseudoplusia* and *Argyrogramma* were placed in a single taxon, as were *Autoplusia* and *Rachiplusia*, and *Plusia [Diachrysia]* and *Agrapha [Allagrapha]*. Those species of *Syngrapha* (*rectangula* (Kirby) and *celsa* (Edwards)) that possessed SV2 on segments TII and TIII, and which also fed as larvae on conifers, were separated as 'Genus no. 11', while those *Autographa* that possessed SV2 on segment A1 (*mappa* (Grote & Robinson), *ampla* (Walker) and *corusca* (Strecker)) were included in *Syngrapha. Autographa* was thus restricted to those species lacking SV2 on segment A1 – *biloba* (Stephens), *californica* (Speyer), *gamma* and *precationis* (Guenée).

Beck (1960) examined the larvae of several European genera of Plusiinae: *Abrostola, Plusia [Diachrysia], Autographa, Chrysaspidia [Plusia], Syngrapha [Euchalcia]* and *Polychrysia*, but also drew no conclusions as to possible affinities.

Although these early larval studies made relatively few hard statements regarding the higher classification of the Plusiinae, they did demonstrate that larvae could be of use taxonomically and paved the way for future research.

Kostrowicki and the Palaearctic plusias

The next major revision of the Plusiinae was performed by Kostrowicki (1961), who studied the Palaearctic fauna, comprising 83 species in 23 genera. *Abrostola* and *Mouralia* were omitted from consideration. Kostrowicki was generally in favour of McDunnough's (1944) arrangement

of the Nearctic fauna but expressed reservations regarding its uncritical application to the Holarctic fauna. Forbes' (1954) reduction of McDunnough's genera to subgeneric status was rejected because this would 'introduce quite unnecessary inequalities with the other subfamilies of [Noctuidae]'. Crumb's (1956) arrangement found more favour but Kostrowicki questioned both the synonymy of *Trichoplusia, Pseudoplusia* and *Argyrogramma*, and the reality of Crumb's 'genus no. 11'.

Kostrowicki then proposed his own phylogeny of the plusias, which he hoped would correct some of McDunnough's and Crumb's parochial errors (Fig. 1). *Argyrogramma* was considered to be the ancestral plusia lineage, which gave rise to three groups of genera. The first consisted of *Anadevidia, Pseudoplusia, Trichoplusia, Chrysodeixis, Macdunnoughia* and *Diachrysia [Thysanoplusia]*. This last genus, for some reason, was omitted from the phylogenetic tree. The second group was characterized by a tendency for the palps to be rather longer than in the other plusiines. One subgroup, *Plusia [Diachrysia], Polychrysia* and *Panchrysia*, was considered to be possibly related to *Diachrysia [Thysanoplusia]*. The second subgroup consisted of a postulated

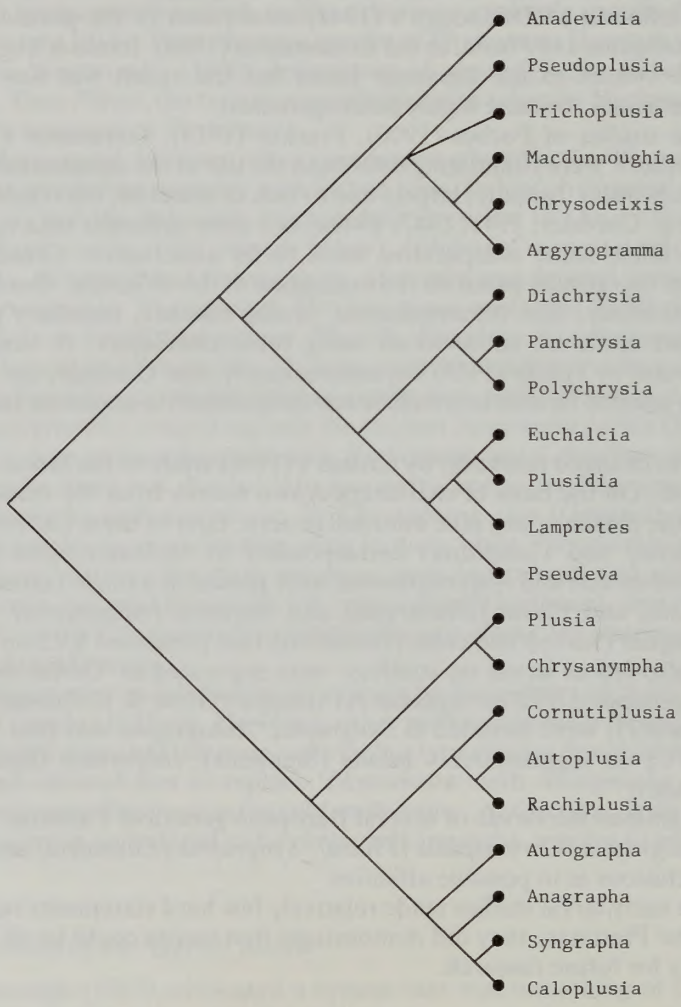


Fig. 1 Phylogenetic tree of Kostrowicki. Originally, his tree depicted supposedly ancestral genera (*Argyrogramma, Diachrysia* (as *Plusia*), *Panchrysia, Euchalcia, Plusia* (as *Chrysaspidia*) and *Autographa*) by thicker branches and branch lengths appear to have been related in some way to degree of anagenetic change. These two aspects were eliminated and only the topology retained in the above figure. Generic names have been changed into their modern forms. (Redrawn from Kostrowicki, 1961.)

ancestral genus, *Euchalcia*, and three derivative genera, *Plusidia, Chrysoptera [Lamprotes]* and *Pseudeva*. Kostrowicki commented on *Eosphoropteryx* in connection with these genera but felt he could not place it within the group because of the distinctive appearance of the genitalia.

The third group to be derived from *Argyrogramma* was based around *Autographa* and *Chrysaspidia [Plusia]*. The latter was considered to have given rise to *Chrysanympha*, while the former had given rise to two groups of genera, both characterized by spinose tibiae. The first consisted of the Nearctic *Autoplusia* and *Rachiplusia* and the Old World genus *Cornutiplusia*. The second included the primarily arctic-alpine genera *Syngrapha* and *Caloplusia*, and the more widely spread Nearctic *Anagrapha*, of which *Syngrapha* was considered to be the ancestral group. Kostrowicki rejected Crumb's (1956) delimitations of *Autographa* and *Syngrapha* because the divisions based upon the larvae were not reflected by differences in the genitalia.

Kostrowicki's scheme showed several important discrepancies compared to the generic interrelationships that had been proposed previously. Several were due to incorrect assignment of species to genera, which then became structurally heterogeneous, or to straightforward misidentification (Ichinosé, 1963*a*; Dufay, 1970*a*). Into the first category fell, for example, the placing of *Autographa aemula* ([Denis & Schiffermüller]), *A. bractea* and *A. argyrosigna* (Moore) in *Chrysaspidia [Plusia]*. The inclusion of *Antoculeora ornatissima* and *Erythroplusia rutulifrons* in *Argyrogramma*, and *Erythroplusia pyropia* (Butler) in *Anadevidia* were due to misidentifications. The male genitalia of *Antoculeora ornatissima* figured have the quadrate saccus typical of *Argyrogramma* and are probably those of *Argyrogramma signata* (Fabricius) (Dufay, 1970*a*: 150, footnote), the only species of *Argyrogramma* (s. str.) to occur in eastern Asia. *'Argyrogramma rutulifrons'* appears to be very closely related to *Argyrogramma circumscripta* (Freyer), and may even be that species. The identity of *'Anadevidia pyropia'* remains a mystery.

The rising influence of larvae: Ichinosé's revisions

Following on from a series of studies of plusiine larval morphology (Ichinosé, 1958*a*; *b*; 1960*a*; 1962*a*), Ichinosé (1962*b*) produced a revision of the Japanese Plusiinae, contemporaneous with Kostrowicki's work. Ichinosé considered that McDunnough had oversplit the subfamily and that many of the characters employed were of little taxonomic significance, particularly the form of the clavus. Instead, Ichinosé preferred the generic assignments suggested by Crumb (1956), although he felt that Crumb had placed too much emphasis on certain characters and thus had reached some dubious conclusions. Although Ichinosé was in favour of using characters drawn from all stages of the life-history in the construction of classifications, at the generic level he predominantly used larval characters, particularly from the chaetotaxy.

Ichinosé recognized twelve genera of Plusiinae. The delimitation of eight of these was uncontroversial and conventional: *Abrostola, Plusidia, Chrysoptera [Lamprotes], Euchalcia, Podioplusia [Anadevidia], Chrysaspidia [Plusia]* and *Syngrapha. Autographa* was divided into three subgenera: *Autographa* (s.str.), *Scleroplusia* [*Macdunnoughia* (s.l.)] and *Erythroplusia*, separated on the basis of the divergent form of the male genitalia but united by a uniform larval morphology. Ichinosé, like Kostrowicki, separated *intermixta* from the remaining species of *Plusia [Diachrysia]* and placed it, together with *daubei* (Boisduval) and *ochreata*, in *Diachrysia [Thysanoplusia]*. The golden wing pattern of *intermixta* and the genus *Plusia [Diachrysia]* was considered to be convergent.

While this reallocation of species left *Plusia [Diachrysia]* more compact and homogeneous, the three species of *Diachrysia [Thysanoplusia]* showed diverse possible affinities. Overall, Ichinosé considered *Diachrysia [Thysanoplusia]* to be much more closely related to *Chrysodeixis* than to *Plusia [Diachrysia]*. However, while the chaetotaxy and skin ornamentation of *intermixta* suggested further affinities with *Podioplusia [Anadevidia]* and *Euchalcia*, the chaetotaxy and external appearance of *daubei* suggested a possible connection with *Chrysodeixis*.

With regard to *Chrysodeixis* itself, Ichinosé followed Crumb (1956), including *Trichoplusia* (and also the species now assigned to the nominal genera *Ctenoplusia (albostriata)* and *Acanthoplusia* (*agnata* (Staudinger) and *tarassota*)).

Ichinosé presented his overall view of the generic relationships in the form of a 'phylogenetic tree' (Fig. 2). Exactly how this dendrogram is to be interpreted is uncertain. It agrees reasonably well with Kostrowicki's tree (Fig. 1), in that the *Polychrysia*-group and the *Autographa*-group arose independently from a *Chrysodeixis-Argyrogramma*-type ancestral form. In both treatments, *Podioplusia [Anadevidia]* was of uncertain position, while Ichinosé's clarification of the positions of *Macdunnoughia* and *Erythroplusia* represented a considerable improvement over Kostrowicki's placings.

Meanwhile, Claude Dufay had been busily publishing a large number of studies on plusiine alpha-taxonomy. He eventually ventured his opinions on the higher classification of the subfamily in his revision of the Madagascan fauna (Dufay, 1970*a*). Following the obligatory discussion of Hampsonian type species designations, Dufay proceeded with a brief discussion of the studies of McDunnough, Kostrowicki and Ichinosé. Like Ichinosé (1963), Dufay disagreed with some of Kostrowicki's generic assignments, particularly regarding *Argyrogramma*. However, he also considered Ichinosé's treatment to be unsatisfactory, for although the groupings were certainly more natural than those of Kostrowicki, several genera (in particular *Chrysodeixis*) were too heterogeneous. Dufay preferred to keep *Trichoplusia, Argyrogramma* and his own *Ctenoplusia* separate from *Chrysodeixis*.

Like Kostrowicki, Dufay's revision was also reviewed in Japan (Sugi, 1972). The major criticism appeared to be Dufay's inclusion of *[Thysanoplusia]* in *Trichoplusia*, which thereby rendered that genus heterogeneous in terms of larval chaetotaxy and skin ornamentation.

Shortly afterwards, Ichinosé (1973) published an upgraded classification of the Japanese plusiines. *Autographa* now included *Macdunnoughia* and *Sclerogenia* as subgenera but the previously included subgenus *Erythroplusia* was elevated to full generic status. *Erythroplusia* comprised two subgenera, *Erythroplusia* (s.str.) and *Antoculeora*, united by characters of the

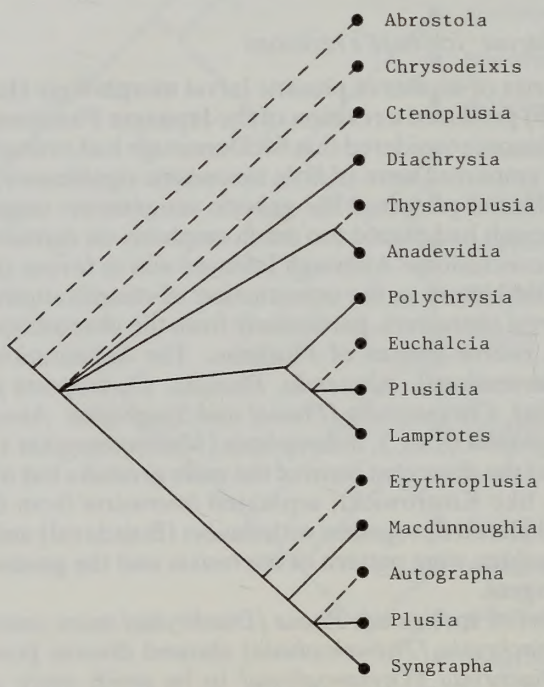


Fig. 2 Phylogenetic tree of Ichinosé. This tree originally consisted of a series of interconnected circles representing the genera. Thus several taxa (*Abrostola, Chrysodeixis, Ctenoplusia* (as *Chrysodeixis*) *agnata, Euchalcia, Thysanoplusia* (as *Diachrysia*), *Erythroplusia* and *Autographa* (s.str.)) were interpreted as ancestral to other genera. These have been placed in the above figure on the ends of 'zero-length' branches, represented by dashed lines. Only two character complexes were included on Ichinosé's tree; larval chaetotaxy type and the presence/absence of lateral tufts on the adult male abdomen. Generic names have been changed to their modern forms. (Redrawn from Ichinosé, 1962*b*).

asymmetrical male genitalia, larval morphology and, tentatively, larval foodplant. However, some possible affinity between *Antoculeora* and *Macdunnoughia* was admitted on the basis of the female genitalia (the sole species of *Antoculeora, ornatissima*, had been previously included by Ichinosé [1962*b*] in *Macdunnoughia*). Ichinosé (1973) remained committed to the view that the *Chrysodeixis-Trichoplusia-Argyrogramma* complex formed a homogeneous group. To recognize a multitude of genera, as had Dufay (1970*a*), was regarded as 'myopic splitting'. However, Ichinosé did relent somewhat and accepted *Chrysodeixis* (with *Pseudoplusia* as a tentative synonym) as distinct from *Argyrogramma*. This latter genus was divided into three subgenera: *Argyrogramma, Trichoplusia* and *Ctenoplusia. Agrapha [Allagrapha]* was synonymized again with *Plusia [Diachrysia]* because the two shared many similarities in the form of abdominal segment 8 in the adult female and in the larval chaetotaxy (but see Eichlin & Cunningham, 1978, and below).

At this point, I will digress briefly from the history of the higher classification of the Plusiinae to examine the problems associated with the type species of the genera *Plusia* and *Diachrysia*, and the application of these names. Up until 1970, most authors had treated *orichalcea* sensu Hübner, designated by Dyar (1902), as the type species of *Diachrysia*. This proved to be a misidentification of *Diachrysia chryson* and resulted in the *orichalcea-intermixta* group of species, which were certainly not congeneric with *chryson* (Kostrowicki, 1961; Ichinosé, 1962*b*), being bereft of a genus. Ichinosé (1973) resolved this by proposing *Thysanoplusia*.

With regard to *Diachrysia* and *Plusia*, most authors had treated these genera as synonyms. In this they followed Grote (1895) in accepting Duponchel's (1829) designation of *chrysitis* as the type species of *Plusia*, a species that was then, and still is, considered to be congeneric with *Diachrysia chryson*. However, they had all overlooked Duponchel's (1826) previous designation of *festucae* as the type species. Thus *Plusia* correctly refers to the *festucae*-group of plusiines and *Chrysaspidia* sinks as a synonym. The next available name for the *chrysitis-chryson* group is *Diachrysia*. However, as noted above (and by Dufay, 1970*a*, and Nye, 1975), this name involves a case of misidentified type species, which should therefore be referred to the International Commission on Zoological Nomenclature under Article 70(b) of the *Code*. Although this will be done in the future, the consensus of all modern works (e.g. Franclemont & Todd, 1983; Bretherton *et al.*, 1984; Skinner, 1984) is that *chryson* is the type species of *Diachrysia*. However, the erroneous inclusion of *orichalcea* in *Diachrysia* is still prevalent (e.g. Bretherton *et al.*, 1984; Skinner, 1984).

To return to the higher classification of the Plusiinae, a totally independent test of all previous arrangements was performed by Nakamura (1974), using characters derived from the hitherto generally ignored pupal stage. Mosher (1916) and Gardner (1948*b*) had examined a small number of species but Nakamura studied 21 species, which allowed him to comment on possible generic interrelationships. Very few of the groupings that he found corresponded to those previously proposed and several cut across the generic boundaries of Kostrowicki, Dufay *and* Ichinosé. Congeners in *Chrysodeixis* (s.l. or s.str.), *Thysanoplusia* and *Acanthoplusia* showed marked differences in pupal chaetotaxy, while, in contrast, species of the genera *Abrostola, Polychrysia, Plusia [Diachrysia]* and *Autographa* (s.str., sensu Ichinosé, 1962*b*) had discrete pupal types, in terms of structure and chaetotaxy. Nakamura compared his results with the generic concepts of Ichinosé (1962*b*), Dufay (1970*a*) and Esaki *et al.* (1971) but refrained from making any formal taxonomic changes of his own.

However, the latest Japanese checklist (Sugi, 1982) has returned to an almost maximally split arrangement. *Lamprotes, Macdunnoughia, Antoculeora, Sclerogenia, Trichoplusia. Ctenoplusia* and *Acanthoplusia* were all treated as distinct genera. Only *Thysanoplusia* (N.B.) and *Puriplusia* were recognized as subjective synonyms, being sunk to *Trichoplusia* and *Macdunnoughia* respectively.

The focus moves back west: Eichlin & Cunningham's reappraisal of the Nearctic fauna

Meanwhile, in the U.S.A., analysis of the American Plusiinae had proceeded along similar lines as had the Japanese fauna a decade earlier. A series of studies of larvae (Eichlin & Cunningham,

1969; Eichlin, 1975) led eventually to a full scale revision of the subfamily on a regional basis (Eichlin & Cunningham, 1978). Like Ichinosé, Eichlin & Cunningham employed both larval and adult characters in the construction of their classification. However, they tried not to place undue emphasis on either data source and so hoped to arrive at an arrangement that was less conservative than that of Ichinosé but not as split as those of McDunnough, Kostrowicki or Dufay. The end result, however, did tend more towards the classifications of the latter three authors (Fig. 3).

Largely on the basis of the form of the larval prolegs, Eichlin & Cunningham divided the subfamily into three tribes, the first occasion on which this taxonomic rank had been used in the Plusiinae. The most primitive tribe, in which the prolegs on A3 and A4 (see Terminology) were fully functional, if albeit slightly reduced, was the Abrostolini, comprising *Abrostola* and *Mouralia*. The latter was seen as a derivative of the former, having more specialized genitalia.

Although Eichlin & Cunningham appeared to treat the Abrostolini as a monophyletic unit, they considered that 'a common ancestor from the *tinctoides* [as opposed to the Abrostolini] line gave rise to the Argyrogrammini [Argyrogrammatini] and Autographini [Plusiini]'. In both of these tribes, the ribs on the larval mandibles bore subterminal processes and the prolegs on A3 and A4 were non-functional.

The Argyrogrammini [Argyrogrammatini] were interpreted as the more primitive tribe because its members retained vestigial prolegs whereas all traces of prolegs had been lost in the Autographini [Plusiini]. Eichlin & Cunningham retained the three genera of McDunnough

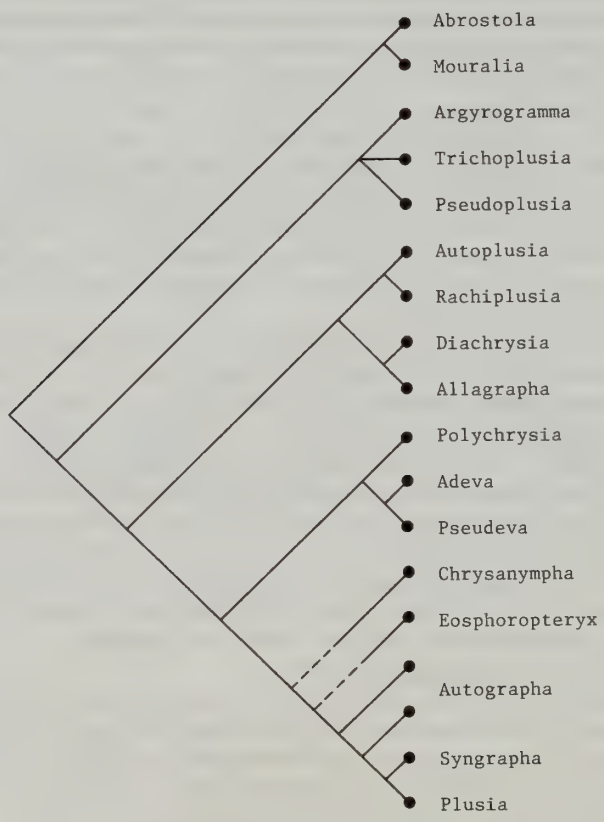


Fig. 3 Generic phylogeny of the Plusiinae according to Eichlin & Cunningham. Their original dendrogram included an anagenetic component that is omitted in the above figure. The positions of *Eosphoropteryx* and *Chrysanympha* were uncertain, as indicated by dashed lines. *Autographa* was interpreted as being biphyletic. The detailed interrelationships of the species of *Autographa* and *Syngrapha* are omitted. (Redrawn from Eichlin & Cunningham, 1978.)

(*Argyrogramma, Trichoplusia* and *Pseudoplusia*), rejecting Ichinosé's (1973) synonymy of the first two, and of the third with *Chrysodeixis*, on the grounds that Ichinosé's larval characters broke down when applied to the Nearctic species. Eichlin & Cunningham preferred to steer a middle course between Ichinosé's larval dominated generic concepts and Dufay's adult dominated system, recognizing, in addition, that the results of Nakamura's (1974) pupal study were at odds with both. However, there were too few Nearctic Argyrogrammini [Argyrogrammatini] to permit Eichlin & Cunningham to draw any significant conclusions regarding the generic limits and interrelationships within the tribe. The three genera were represented on the phylogenetic tree (Fig. 3) as a trichotomy, although *Pseudoplusia* was considered to be the most advanced genus because it had lost the lateral abdominal tufts in the male (present in *Trichoplusia* and *Argyrogramma*), retained the mandibular processes (lost in the other two genera) and had a unique highly-elongate apex to the corpus bursae.

The third tribe of plusiines, the Autographini [Plusiini], contained the balance of the American genera, 12 in all. Eichlin & Cunningham refrained from subdividing the group using adult characters because of the high degree of larval uniformity. The first group of four genera to branch off the main phylogenetic line were characterized by the retention of separate pinacula for setae SV1 and SV2 on A2. In all other genera of Autographini [Plusiini] examined, these two pinacula were at least partially fused. Using the degree of separation of the V1 setae on A1–4 (supposedly linked to the time elapsed since the prolegs were lost on A3–4), *Autoplusia* was interpreted as the most primitive genus, followed by *Rachiplusia, Plusia [Diachrysia]* and *Allagrapha*. However, this arrangement was complicated by the presence of tibial spines, long believed to be an advanced character, in the former two genera.

With regard to *Allagrapha*, Eichlin & Cunningham rejected its synonymy with *Plusia [Diachrysia]*. In particular, the presence of a raduloid (a ridged structure on the larval hypopharynx) in the two species of *Allagrapha* (absent in the Nearctic *Plusia [Diachrysia] balluca* Geyer, the only species of the genus examined as a larva), features of the male genitalia and a strong superficial similarity were used to argue full generic status for *Allagrapha*.

The next section of Eichlin & Cunningham's tree was highly tentative because the larvae of four of the five genera (*Adeva, Pseudeva, Eosphoropteryx* and *Chrysanympha*) were not known. The fifth, *Polychrysia*, was considered to form the next branch off the main stem, because the larva retained the primitive arrangement of the V setae mentioned above. *Adeva* and *Pseudeva* were placed together because of the very reduced clavus and associated with *Polychrysia* because of the overall similarity of their genitalia. *Chrysanympha* and *Eosphoropteryx* were inserted next on the tree but their exact relationships were left open.

Eichlin & Cunningham noted that *Autographa*, while structurally uniform in the male and female genitalia, could be subdivided into two lineages by the presence or absence of seta SV2 on A1, presence being the derived condition. The final two genera, *Syngrapha* and *Chrysaspidia [Plusia]*, were well defined. The former had spinose tibiae and the latter had uniordinal crotchets (unique in the Plusiinae) and an unusual larval mandible. *Syngrapha* was further subdivided into a number of species groups, one of which (including *Palaeographa* and *Caloplusia*) was characterized by the presence of seta SV2 on TII and TIII, a feature unique within the Noctuidae (see also Crumb, 1956).

Eichlin & Cunningham concluded by noting that the three major classifications, their own and those of Kostrowicki and Ichinosé, were not particularly different in terms of the major evolutionary lineages they depicted. They considered this to be highly significant, given the more or less exclusive nature of the faunas upon which each was based. Nevertheless, Eichlin & Cunningham felt that there was still a great gap in the knowledge of the tropical plusiines and that this needed to be filled before a synoptic classification of the subfamily could be established.

The latest North American checklist (Franclemont & Todd, 1983) explicitly followed Eichlin & Cunningham's tribal and generic assignments but within a few (unexplained) changes. *Trichoplusia oxygramma* was removed into *Agrapha*, under which was synonymized *Ctenoplusia* and *Acanthoplusia*. *Allagrapha aereoides* Grote (as *aeroides*) was put back into *Diachrysia* (following McDunnough, 1944) and *Adeva* was synonymized with *Euchalcia* (following Kostrowicki, 1961). *Anagrapha* was resurrected for the divergent *falcifera*.

Return to the east: Chou & Lu's phylogeny

The late 1970s saw a surge of interest in the Plusiinae of China. Following a series of descriptive papers (Chou & Lu, 1974; 1978; 1979*a*; *b*), which included many inadvertent synonyms due probably to poor access to previous publications on the subfamily, Chou & Lu (1979*c*) published a summary of their ideas on the higher classification of the Plusiinae (Fig. 4).

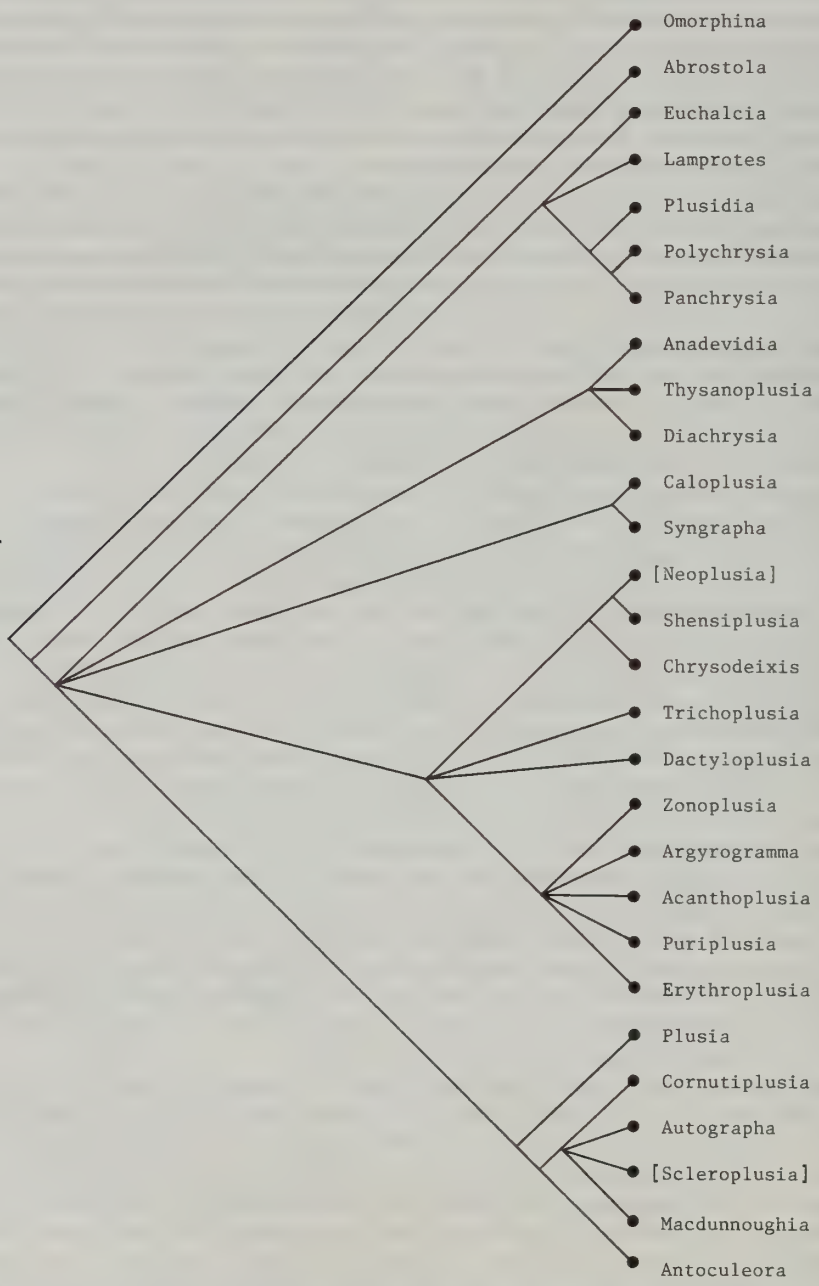


Fig. 4 Phylogeny of the Plusiinae according to Chou & Lu. Seven tribes were recognized (Omorphinini, Abrostolini, Euchalciini, Plusiini [sic], Caloplusiini, Argyrogrammini [sic] and Autographini) corresponding to the seven major lineages. *Neoplusia* and *Scleroplusia* are synonyms of *Chrysodeixis* and *Macdunnoughia* respectively and are placed in square brackets. Generic names have been converted into their modern forms. (Redrawn from Chou & Lu, 1979*b*.)

Seven tribes were recognized. The most primitive was considered to be the Omorphinini, comprising only *Omorphina aurantiaca*. Chou & Lu acknowledged the earlier suggestion (Kostrowicki, 1961) that *Omorphina* ought probably be transferred to the Erastriinae [Acontiinae], but they chose to retain it in the Plusiinae pending more detailed study. The next tribe, the Abrostolini, contained only *Abrostola*. *Euchalcia, Chrysoptera [Lamprotes], Plusidia, Polychrysia* and *Panchrysia* were placed in the Euchalciini, while the [Plusiini] comprised *Plusia [Diachrysia], Thysanoplusia* and *Anadevidia*. The Caloplusiini included *Syngrapha* and *Caloplusia*. By far the largest tribe was the Argyrogrammini [Argyrogrammatini], consisting of four subgroups; two contained only single genera (*Trichoplusia, Dactyloplusia*), a third included *Neoplusia [Chrysodeixis], Shensiplusia* and *Chrysodeixis*, while the fourth consisted of a pentachotomy subtending *Zonoplusia, Argyrogramma, Acanthoplusia, Puriplusia* and *Erythroplusia*. These last two genera were placed near *Acanthoplusia* despite lacking vestigial larval prolegs (also absent in *A. agnata*; Ichinosé, 1962*b*) and anal tufts in the male. If *Puriplusia* and *Erythroplusia* are excluded, then the Argyrogrammini [Argyrogrammatini] is more or less equivalent to *Chrysodeixis* (s.l.) (sensu Ichinosé, 1973).

The final tribe, the Autographini [Plusiini], included six genera in three subgroups. *Chrysaspidia [Plusia]* represented the most basal branch, followed by *Autocureola* [sic, *Antoculeora*]. The four remaining genera (*Autographa, Cornutiplusia, Scleroplusia [Macdunnoughia]* and *Macdunnoughia*) were treated as a tetrachotomy. *Cornutiplusia* was considered to be identical to *Autographa* (except for the spined tibiae) and *Autocureola [Antoculeora]* was interpreted as the most advanced genus.

No resolution of the tribal interrelationships was attempted. Several of the tribes, notably the [Plusiini], were distinctly phenetic in construction. Chou & Lu preferred to group genera on a limited number of superficial characters of doubtful taxonomic significance (see below), which resulted in a number of generic misplacements. Nevertheless, the overall classification had a great deal in common with those proposed previously.

Ronkay (1982), in a review of the Korean fauna, also accepted the general findings of Kostrowicki, Ichinosé and Eichlin & Cunningham. However, he disagreed on several points. Ronkay considered Ichinosé's interpretation of *Macdunnoughia* as a subgenus of *Autographa* was incorrect and he reinstated the former to generic level. Chou & Lu's (1974; 1979*c*) treatment of *Puriplusia* as a good genus was also disputed and Ronkay, agreeing with Dufay (1977), reduced *Puriplusia* to subgeneric rank within *Macdunnoughia*. The generic assignments within the Argyrogrammatini were also considered problematical and, pending a full tribal revision, Ronkay chose to retain the genera *Trichoplusia, Ctenoplusia, Chrysodeixis* and *Argyrogramma* according to Dufay's usage.

Holloway (1985), in his study of the Bornean fauna, also maintained *Chrysodeixis* and *Ctenoplusia* as distinct, pending further investigation. *Thysanoplusia, Zonoplusia* and *Dactyloplusia* were also treated as good genera but several plusiine species remained unassignable to current genera. Holloway followed the practice of Dufay (e.g. 1972; 1974) in placing such species in '*Plusia*' s.l. Although this approach is unsatisfactory, it was the best that could be achieved for these species until a comprehensive revision of the subfamily, and particularly the Argyrogrammatini, is performed.

Kljutshko's 'cladistic' analysis of the Plusiinae

The most recent studies to consider the higher classification of the Plusiinae are those of Kljutshko (1985*a*; *b*). For the first time in plusiine systematics, cladistic techniques were overtly employed to analyse a data set of 32 characters, drawn from larval, pupal and adult morphology. The result was a cladogram (Fig. 5) based upon the 24 characters that Kljutshko considered to be the most well-founded. However, the analysis was fundamentally flawed in such ways as to render most of the resolution of the cladogram spurious and thus invalidate most of the conclusions drawn from it.

First, and most crucial, the cladistic methodology was misapplied. Although some groups were supported by putative synapomorphies (e.g. *Ctenoplusia* and *Acanthoplusia* on the basis of

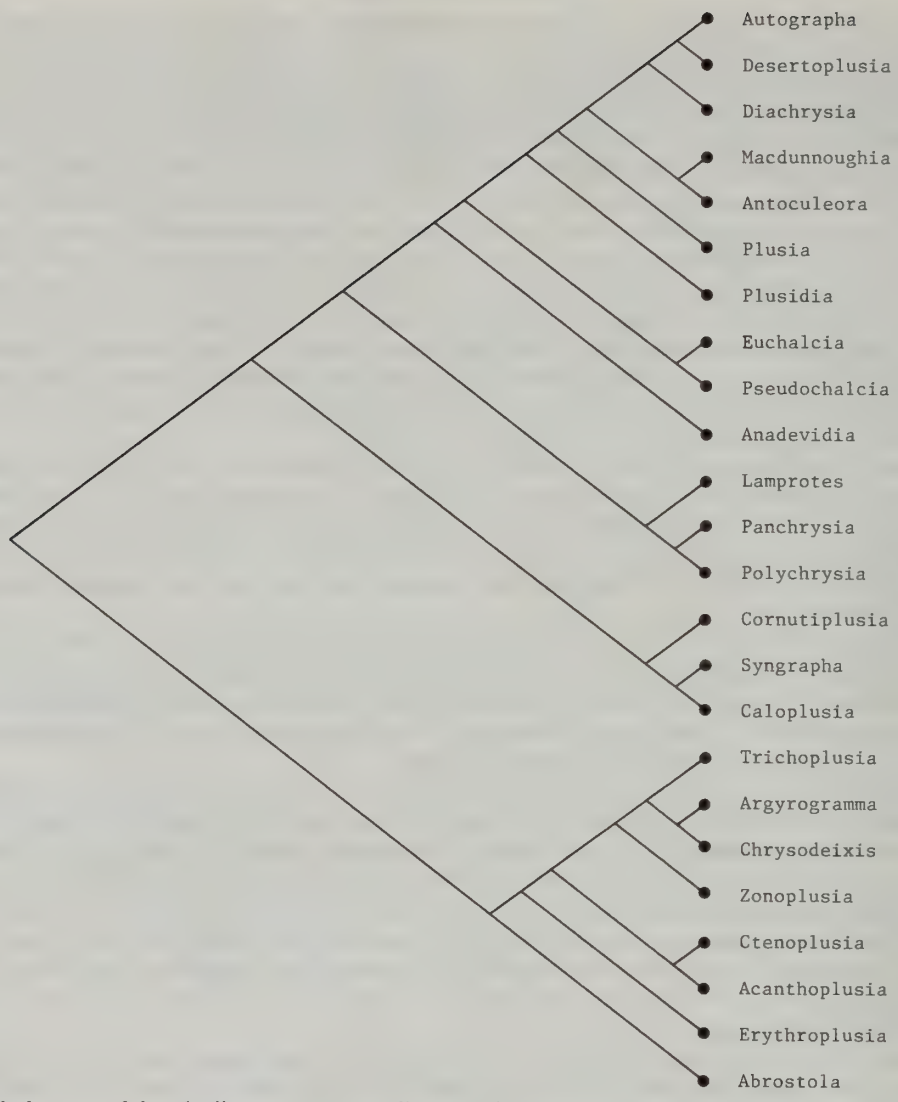


Fig. 5 Cladogram of the plusiine genera according to Kljutshko. (Redrawn from Kljutshko, 1985*a*, *b*.)

blade-like setae on the valve), others were distinguished and delimited using symplesiomorphies. For example, *Autographa* and *Desertoplusia* were united, and separated from *Diachrysia* on the basis of a long harpe, the plesiomorphic state for his character 22. Similarly, the members of the 'clade' *Autographa-Antoculeora* were distinguished from *Plusia* by the presence of biordinal crotchets on the larval prolegs (Kljutshko's character 6). However, all other known plusiine larvae have biordinal crotchets and it is more parsimonious (and in keeping with previous authors' conclusions) to treat the uniordinal condition in *Plusia* as autapomorphic for this genus. This would appear to be a failure to employ the outgroup criterion correctly.

If character 6 is reinterpreted and all the groups characterized by symplesiomorphies collapsed to form polytomies, then a much less well-resolved cladogram results (Fig. 6). Three tribes were recognized by Kljutshko: the Abrostolini, the Argyrogrammatini (including *Erythroplusia*) and the Plusiini. The last consisted of three subtribes: the Plusiina (including *Anadevidia*), the Caloplusiina and the Polychrysiina. Of the tribes, the Abrostolini and the Argyrogrammatini were sister-groups, in contrast to every other phylogeny that had been previously proposed for the Plusiinae. This relationship was based upon the possession of a

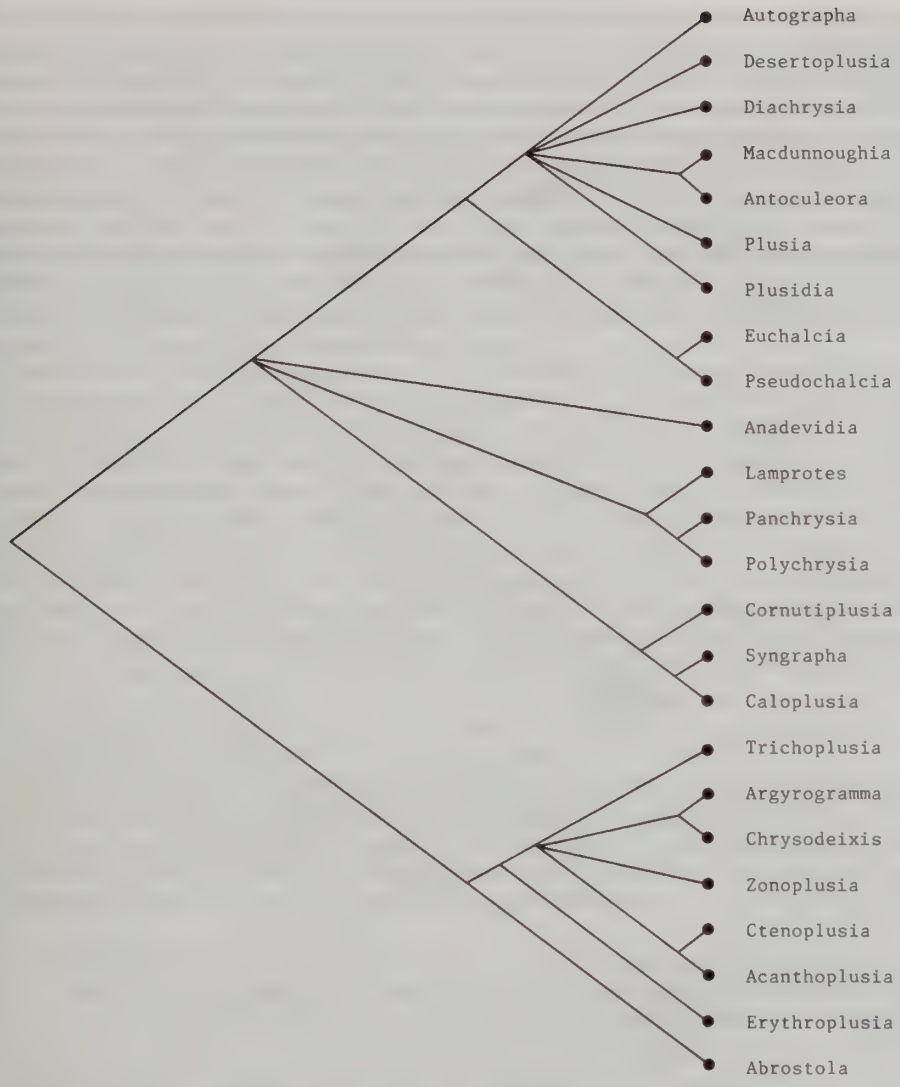


Fig. 6 Cladogram of the Plusiinae derived from the data set of Kljutshko (1985*b*) following the correct application of cladistic methodology. Many of the taxa in Fig. 5 were delimited by plesiomorphic character states. Their elimination results in numerous polytomies.

finer, hair-like seta SD1 on A9 of the larvae (this state is also convergently derived in *Cornutiplusia*).

However, even the reduced cladogram shown in Fig. 6 is defective. The reason for this lies in the characters that Kljutshko used, many of which are insubstantial and nugatory (e.g. the forms of the clavus and harpe, and the origin of the ductus bursae on the corpus bursae), and all of which appear to have been culled from the works of other authors. The result suffers from deficiencies similar to those in the 'phylogenetic tree' of Chou & Lu (1979*c*).

Within the constraints imposed by Kljutshko's choice of characters, the following additional modifications can be made to the character analysis (albeit in the light of my own analysis described below). In addition to character 6, the polarity of character 26 should be reversed because the absence of a signum is plesiomorphic for the Plusiinae as a whole. Since the absence of an epicranial suture in the pupa characterizes the members of both the Plusiini and the Argyrogrammatini (see also Nakamura, 1974), this state can be reinterpreted as synapomorphic

for these two tribes. It also follows from this that the polarity of character 4 (SD1 on larval A9) should be reversed as well. I also reject characters 12 (only *Euchalcia gerda* and *E. serraticornis* Dufay [Dufay, 1968] have serrate antennae, and only *Lophoplusia* has bipectinate antennae, none of which were examined in Kljutshko's study), 18 (if the dorsal abdominal tuft on the adult A2 is reduced in any genus, it is in *Plusia*, not *Syngrapha*; see almost any author on the Plusiinae) and 29 (the position of the ostium bursae on A8) as having any significance. The final result of these changes is shown in Fig. 7 and represents the only informative structure present in Kljutshko's original cladogram (Fig. 5).

As alluded to above, the Argyrogrammatini and Plusiini have a sister-group relationship but a trichotomous one that includes *Erythroplusia* as an unplaced genus. The members of the Argyrogrammatini are united by the presence of subdorsal tufts on A5–6 in the male but form an

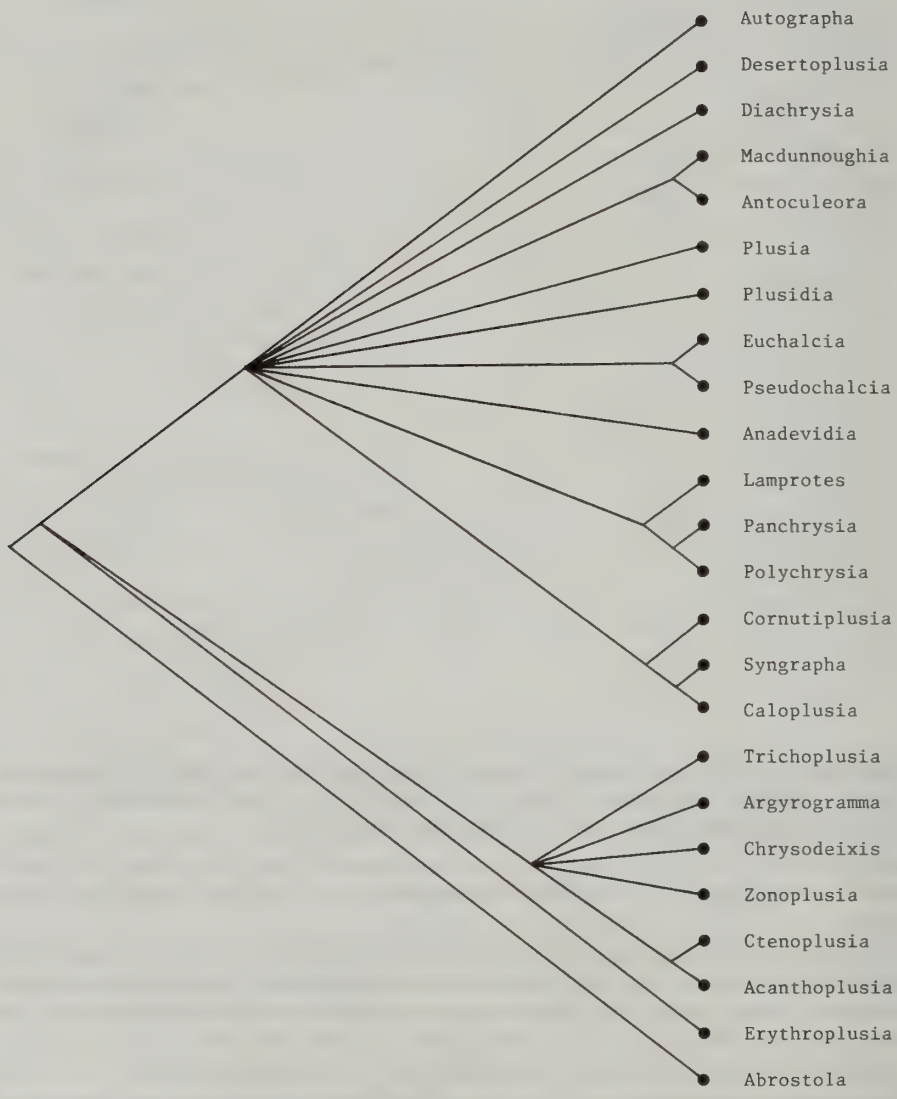


Fig. 7 Cladogram of the Plusiinae derived from the data set of Kljutshko (1985*b*) following further character analysis. Several characters (see text) were reinterpreted by the correct application of the outgroup criterion for determining character polarity and several more were omitted. The resulting cladogram represents the sum total of the information in Kljutshko's data set. There are extensive polytomies and few informative groups. Note, however, the monophyly of the Argyrogrammitini, *Ctenoplusia* (s.l.) and the clade *Macdunnoughia* + *Antoculeora*.

apical pentachotomy, in which the only further resolution is the union of *Ctenoplusia* and *Acanthoplusia* on the basis of blade-like setae on the valve. The Plusiini are characterized by a normal seta SD1 on A9 and the total loss of prolegs in the larvae. The 16 constituent genera of this tribe also form a highly polytomous apex, with no fewer than ten branches. *Euchalcia* and *Pseudochalcia* are united by the form of the juxta, while *Macdunnoughia* and *Antoculeora* share a weak uncus that is not apically hooked. *Polychrysia, Lamprotes* and *Panchrysia* are placed together by the possession of very long palps and probosces but form a trichotomy. *Cornutiplusia, Syngrapha* and *Caloplusia* are united by the shared presence of tibial spines, while the latter two genera are treated as sister-groups because they both display a juxta with an apical process (the same state that unites *Euchalcia* and *Pseudochalcia*). All the genera have autapomorphies that will not be considered further here, with the exception of *Chrysodeixis, Ctenoplusia, Autographa, Polychrysia, Lamprotes* and *Syngrapha*.

I have conducted the preceding re-analysis of Kljutshko's cladogram in order, not to deride his work, but to congratulate him. He, amongst all previous authors (with the possible exception of Ichinosé, 1962*b*), has produced a thoroughly explicit analysis that is open to examination and constructive criticism. Many other authors (notably Kostrowicki [1961] and Chou & Lu [1979*c*]) chose not to state the exact reasons (if any) for the conclusions they reached. Even Eichlin & Cunningham (1978) only explicitly stated some of the characters they used in order to reach their final classification, which rendered many parts of their 'phylogenetic tree' immune to criticism. Thus, despite the errors in analytical procedure and his reliance upon a small number of largely superficial characters (see below), Kljutshko did produce an arrangement for which his reasoning was clear and in which the characters used to delimit each taxon were unambiguously stated.

Two unconventional approaches -

All the studies discussed above investigated the external morphology of the larvae, pupae and adults, with primary attention being focussed on the cuticular structures of the male and female genitalia. There have been two further studies that considered more unconventional organ systems. Both deal with only a very restricted sample of species but the results do appear to corroborate some aspects of previous classifications. For this reason, they will be discussed in detail.

Callahan (1960) examined the structure of the male and female reproductive tracts in eight species of Plusiinae, paying particular attention to those parts that operate in the formation and insertion of the spermatophore. Thus, in addition to the aedeagus and the corpus bursae, Callahan also examined the cuticular simplex (the part of the male genitalia between the testes and the aedeagus that is normally removed in genitalia preparations) and the spermatophore itself.

The species were found to fall into two distinct groups. Group I included *Autographa biloba, Agrapha [Allagrapha] aerea* and *Rachiplusia ou* (Guenée), and thus contained only and all the members of the Plusiini studied. They were characterized by a spermatophore with a short, heavy collum and large cap, a short aedeagus without a sclerotized bulbous lock and a cuticular simplex with a short, broad constrictor muscle. In contrast, the species of Group II had a medium or long, narrow collum, a small spermatophore cap that fits tightly at the apex of the corpus bursae where the ductus seminalis arises, a sclerotized bulbous lock on the inner wall of the uneverted vesica, a long aedeagus and a constrictor muscle that is elongate and tapered at the basal end. This group included *Pseudoplusia includens, Trichoplusia ni, T. oxygramma* (Geyer), *Argyrogramma verruca* and *A. basigera* (Walker), and thus corresponded to the Argyrogrammatini. Although there were characters that might have allowed subdivision of these groups (particularly states that might group *Autographa* and *Agrapha [Allagrapha]* to the exclusion of *Rachiplusia*; and *Trichoplusia* and *Pseudoplusia* to the exclusion of *Argyrogramma*), such analysis was precluded by the lack of an outgroup by which to polarize the transformation series. However, the results of Callahan's study did corroborate the tribes subsequently proposed by Eichlin & Cunningham (1978).

The second 'unconventional' morphological study examined the musculature of the male genitalia (Bayer, 1965). The results of a previous (unreferenced) study of the valves of 25 South African plusiine species suggested that they could be divided into five groups. Four (A–D) corresponded to *Cornutiplusia, Chrysodeixis, Ctenoplusia* and *Trichoplusia* (part). The fifth group, E, included two species of *Thysanoplusia*, two species of *Trichoplusia* (*sestertia* (Felder) and *arachnoides* (Distant)) and *'Plusia' tetrastigma* (Hampson) (which may properly belong in *Trichoplusia* [Dufay, note in BMNH collection]). Finally, there were four unplaced species: two *Abrostola* and two *Trichoplusia* (*transfixa* (Walker) [*vittata* (Wallengren)] and *obtusisigna* (Walker)). The distinction between groups D and E was noted as not being very marked. Bayer then proceeded to examine the male genital musculature of six species in greater detail: *Cornutiplusia circumflexa, Chrysodeixis acuta* (Walker), *Ctenoplusia limbirena, Trichoplusia angulum* (Guenée), *T. transfixa [vittata]* and *Thysanoplusia orichalcea*. (The first species was placed in *Syngrapha*, the remainder in *Plusia*.)

Although a number of structural differences were found to suggest *Cornutiplusia, Chrysodeixis* and *Trichoplusia vittata* might be separated from the other three species, no characters were found that would enable their grouping into higher taxa. Nevertheless, the discovery of quite major musculature changes, such as the loss of entire muscles or marked differences in insertions, does suggest that the genital musculature has great potential in higher classification.

The position of the Plusiinae within the Noctuidae

When the Plusiinae were first proposed as a group (Boisduval, 1828), they were placed as part of a linear sequence between the Noctuelidi, a conglomerate of the presently recognized trifine subfamilies, and the Heliothidi. Guenée (1841) and Duponchel (1844) retained a tentative relationship with the Heliothidi, but also favoured an affinity with the Calpidi. In contrast, Herrich-Schäffer (1845) removed the Plusidae [sic] from any association with the Heliothidae, and placed them in a part of his sequence that included the Metoponidae and Erastridae.

Guenée's second classification (1852–4) divided the noctuids into two main phalanges based on hindwing venation. The Plusidae were included in the tribe Variegatae of the phalange Quadrifidae, together with such families as the Eurhipidae [Euteliinae], Calpidae and Gonopteridae. Thus, in his revised classification, Guenée retained a relationship between the Plusidae and the Calpidae, but rejected a connection with the Heliothidae, which was placed in the phalange Trifidae.

Packard (1869) also employed a two-way split of the Noctuidae but based upon the shape of the clypeus and the antennal form, rather than wing venation and palps. Thus, he included the plusiines in the Noctuinae with the trifine noctuids, rather than in the Catocalinae, with the quadrifines. Grote (1882; 1895) continued this usage, which reassociated the Plusiinae with the Heliothinae, but also placed the Calpinae nearby, together with the Stiriinae, which were considered to be closely related to the heliothines.

Both Tutt (1891–2) and Hampson (1893–5) preferred to use versions of Guenée's (1852–4) second classification. Tutt (1902) subsequently modified his position to approximate that of Grote (1895) by considering the plusiines to be a highly developed group of heliothines. The reduced larval prolegs of most plusiines, by which they were associated with the Calpinae and other quadrifines with semi-looper larvae, were explained as the result of convergent evolution.

In contrast, Hampson (1902) had completely reappraised his classification of the Noctuidae and this culminated in a system that was at once to revolutionize and stultify noctuid higher systematics. By classifying the noctuid moths into semi-artificial assemblages, using a small number of characters applied absolutely, Hampson succeeded in creating a series of subfamilies between which there were no possibilities for higher level relationships. Noctuid higher classification, which had been hierarchical to varying degrees since Boisduval (1828), had been reduced to a single tier system in one fell swoop. The Plusiinae were no longer seen as having closer relationships with some subfamilies than others; now they were just one among 15 equals. Even the major division between trifine and quadrifine hindwing venation was not reflected in the classification.

This attitude towards higher level classification was further institutionalized by the authors of 'Seitz', but this unfortunate state of affairs did not long go unchallenged. Richards (1932) conducted a detailed comparison of the morphology and evolution of the tympanal organ in which, in addition to dividing the Noctuidae into a number of subfamilies, he also suggested possible interrelationships between the subfamilies in the form of a phylogenetic tree. The Plusiinae were found to exhibit a very distinct type of tympanal organ, with a double tympanal hood and a greatly enlarged pocket IV, intimately fused to the tympanal air sac. The subfamily Stictopterinae were found to possess a tympanal hood with a ventral lobe and a pocket IV which, while of normal size for a noctuid, was intimately fused with the air sac as in the Plusiinae. On the basis of these similarities, Richards proposed that the Plusiinae had been derived via the Stictopterinae from the higher Erebinae [Catocalinae] of group IV (including *Euparthenos* Grote and *Zale* Hübner). This relationship between the Stictopterinae and the Plusiinae was accepted by all subsequent authors, Forbes (1954) even going so far as to suggest that the two subfamilies might better be treated as one. Eichlin & Cunningham (1978) also found no fault with this suggestion and used it in order to construct their 'prototype' plusiine. One of the major conclusions of the work detailed below is that the belief in such a stictopterine-plusiine sister-group relationship is erroneous.

Taxa examined

The 400 or so species of Plusiinae are currently classified into about 30 to 50 genera, depending upon the degree of taxonomic 'splitting' adopted. To attempt to maximise the resolution of the supraspecific relationships and to test the validity of many of the synonymies, 45 nominal genera were selected for analysis, all of which have been in recent use. The type species of each (Appendix 1) was employed as an exemplar taxon and although difficulties were encountered in coding some characters that displayed intrageneric variation, this approach was adopted to minimise ambiguity in the application of generic names. In addition, two other plusiine taxa were included: *Palaeographa* Kljutshko, which had been proposed only as a subgenus of *Syngrapha* Hübner; and *Autographa bractea* ([Denis & Schiffermüller]), to represent the more derived lineage of *Autographa* Hübner, a genus considered to be biphyletic by Eichlin & Cunningham (1978) (but see Clade analysis).

Several plusiine generic level taxa were omitted. These are given in Appendix 2, together with the reasons for their rejection. Unjustified emendations and subsequent misspellings are not included. Several additional plusiines, other than the type species, were dissected for a variety of reasons.

Antoculeora locuples (Oberthür, 1881): the BMNH series of *Antoculeora ornatissima* may include one or more of this taxon, which were dissected in error. However, this did not affect the present study for the putative *A. locuples* specimen (1 ♂) did not differ from the putative *A. ornatissima* in any character scored in this study.

Autoplusia olivacea (Skinner, 1917) (Fig. 81): dissected by chance from a mixed series with *A. egena* but which proved useful in confirming several character states and transformation series.

'Syngrapha' gammoides (Blanchard, 1852) (Figs 82, 83): dissected for another study and used in the present investigation because the male genitalia were less specialized than those of either *A. egena* or *A. olivacea* and thus aided the clarification of several characters. *'S.' gammoides* is almost certainly a species of *Autoplusia*. This genus is currently being investigated by Fernando Navarro (Tucumán) and pending the results of his study, I will refer to this moth as *'Syngrapha' gammoides*.

Chrysodeixis argentifera (Guenée, 1852) (Fig. 40); *C. illuminata* (Robinson, 1968) (Fig. 41); *C. kebea* (Bethune-Baker, 1906) (Fig. 42): the type species of *Chrysodeixis, chalcites*, has extremely modified sternal hair pencils in the male (see Terminology) and it proved impossible to score characters 80–95 for this species. Three further species of *Chrysodeixis* were dissected in order to determine the nature of the modification in *C. chalcites*. *C. kebea* and *C. illuminata* were found to be almost as extreme as *C. chalcites* but *C. argentifera* possessed a typical pair of sternal hair pencils. Characters 80–95 were thus scored from this latter species.

Plusiopalpa shisa Strand, 1919: only a single male of the type species, *P. dichora*, was found in the BMNH collection, and so a male of *P. shisa* was also dissected to check leg and abdominal characters. The

identification of this specimen as *P. shisa* rested solely on its Taiwanese origin. A study of the genitalia may demonstrate this species to be synonymous with *P. adrasta* (Felder).

In addition, 11 outgroup taxa were analysed (Appendix 1) and were chosen on the following bases.

Stictoptera/Lophoptera: to represent the two main lineages (Holloway, 1985) of the subfamily Stictopterinae, which is considered by many to be closely related to the Plusiinae. The BMNH series of the type species of *Lophoptera, L. squammigera*, appears to be mixed (J. D. Holloway, pers. comm.) but this will have no effect on the present study.

Paectes/Anuga: to represent the subfamily Euteliinae, considered by Holloway (1985) to be a more likely candidate for the sister-group of the Stictopterinae. *Paectes cristatrix* was used inadvertently instead of the type species, *P. pygmaea* Hübner.

Magusa: this genus superficially resembles *Stictoptera* and may be related to it.

Calophasia/Cucullia: to represent the subfamily Cuculliinae, which share with the Plusiinae the character state of lashed eyes.

Diloba/Brachionycha: Diloba has been associated in the past with the Plusiinae (amongst many other groups, see Kitching, 1984) and this relationship was to be tested. It has also been suggested that *Diloba* is related to the cuculliine tribe Psaphidini and thus *Brachionycha* was included, as the only member of this tribe sufficiently well represented in the BMNH collection to be utilized.

Chalcopasta/Oncocnemis: the former genus has a similar facies to members of the plusiine genera *Thysanoplusia* and *Diachrysia*, and a relationship between the amphipyrine tribe Stiriini (of which *Chalcopasta* is a member) and the Plusiinae has been very tentatively suggested. However, Hogue (1963), in his revision of the Stiriini, strongly favoured a relationship between this tribe and the cuculliine tribe Oncocnemidini, hence the inclusion of *Oncocnemis* as an outgroup in this study.

Several other genera were initially examined but were rejected because they appeared to have no close affinity with the Plusiinae – *Plusiophaes* Prout, *Scoliopteryx* Germar, *Xylena* Ochsenheimer, *Lithophane* Hübner, *Nycteola* Hübner and *Pseudoips* Hübner. In addition, two stictopterines, *Odontodes* Guenée and *Nigramma* Walker (now a synonym of *Gyrtona* Walker; Holloway, 1985) were scored but rejected as redundant to the problem at hand.

All taxa were scored from specimens held in the BMNH collection except for the following:

Loboplusia vanderweelei holotype ♂, paratype ♂: Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands;

Autographa pokhara Dufay holotype ♀ (= *Loboplusia vanderweelei* ♀): Zoologische Staatssammlung, Munich, West Germany;

Shensiplusia nigribursa holotype ♀: Northwestern College of Agriculture, Wukung, China. This species was not examined; however, as many characters as possible were scored from the original description and accompanying diagrams of wing pattern and female genitalia (Chou & Lu, 1974).

Terminology

In this section, I shall define those morphological terms that may have ambiguous usage within the Lepidoptera or that I have introduced in this study. They concern mainly internal structures, the male sternal hair pencils and the male genitalia. Unambiguous or universally accepted terms are omitted. Genitalic terminology generally follows Klots (1970); wing venation follows Neilsen (1985). Thoracic segments are termed TI–III (Roman numerals) and abdominal segments A1–8 (occasionally –A10 with reference to larvae). The abdominal tergites and sternites are termed T1–8 (note Arabic numerals) and St1–8 respectively.

Wings. The scale tooth is a triangular tuft of scales projecting from the tornal angle of the forewing. In the males, the frenulum consists of a single bristle formed by the fusion of several setae. In most of the species examined in this study, the female frenulum consists of three setae. The innermost seta is termed 1, the outermost 3 (Fig. 124). Reduction in number generally results from the loss of seta 1 first, and seta 2 next. Whether reduction is by loss or by fusion is often difficult to assess. In those species with four frenular setae, it is unknown whether the extra seta represents a '0' or a '4'. Crossveins are identified by the main veins between which they run, labelled in lower case. Thus m_1–m_2 is the cross vein between M_1 and M_2. The terms lower, middle and upper discocellular veins are avoided.

Labial palps. The apical 'pit organ' of segment 3 is here termed 'vom Rath's organ' (Rath, 1887), following Kristensen (1984). The sensilla contained in the pit have been thought to be chemoreceptors, thermoreceptors or hygroreceptors (Chauvin & Faucheux, 1981), but have recently been shown to be sensitive to carbon dioxide (Bogner *et al.*, 1986).

External thoracic structure. The tegulae (Figs 164–167) are interpreted as having two arms. The dorsal arm is broad and usually bluntly pointed or rounded, and protects the forewing base dorsally. The ventral arm is thin and covered in microspines apically. It curves out and under the wings, where its spinose apex may aid in holding the wings in position at rest.

Legs. The basitarsal comb is a row (or rows) of specialized setae (Figs 178–181) on the inner subventral edge of the hindbasitarsus of many male argyrogrammatines. The function of these combs is still unknown, although their partial correlation with the dorsolateral hair tufts (see below) suggests that they may be used for grooming. They do not seem to be absolutely essential, however, for although all species with combs have tufts, not all species with tufts have combs. The genus with the most highly developed tufts of all, *Chrysodeixis*, lacks combs.

In general, there are three discrete rows of setae along the ventral surface of the tarsi in plusiines. The central row is termed the V (ventral) row, the lateral rows SV (subventral). Additional SD (subdorsal) and D (dorsal) setae may also occur.

Internal prothoracic structure. The internal structure of the ventral part of the prothorax of a typical plusiine is illustrated in Fig. 211. The ventral midline (discrimen) is inflected to form two large, curved processes that form the dorsal arms of the prothoracic furca. Basally, these are produced posteriorly to form a thin, apically bifurcate spinisternum (not shown). The dorsal furcal arms are produced subventrally into broad, rounded projections termed the subventral (SV) furcal arms. To these structures are attached several of the foreleg muscles. The apices of the dorsal arms are connected on each side to the dorsal edges of the epimera by a cuticular membrane. This structure may possess a dorso-ventral ridge running from the epimera to the SV furcal arms (Fig. 212).

Male abdomen A1–7. Terminology for the trifine hair pencil components follows that of Birch (1972*a*; *b*). Dorso-lateral hair tufts occur in many male Argyrogrammatini. The tufts have greasy, matted, apparently secretory patches of scales at their bases and are assumed to be scent organs, presumably involved in courtship. Those of A7 are occasionally enclosed in cuticular folds of various types. All are easily removed during normal preparatory procedure for slide mounting and then often go undetected.

Male A8 and sternal hair pencils. The modifications to A8, concerning the elaboration of the sternal hair pencils of male plusiines, are very complex and still incompletely understood. The plesiomorphic condition was presumably a simple quadrate T8 and St8. In many of the genera examined, including all of the plusiines and several of the outgroups, T8 was cruciform, or bilobate, in which the anterior arms had been reduced or lost. The shape of T8 is often species specific (Dufay, 1970*a*) but although much variation was found in this study, no patterns to the different forms could be discerned and thus no characters were derived from it.

St8 appears first to have evolved a central, posterior, desclerotized area giving rise to a U-shaped sclerite in which the arms point posteriorly. Between these are developed a patch of secretory, setose scales. This desclerotized area is then invaginated as two pockets (more rarely one), in which are located the sternal hair pencils. These pockets are often fused, partially or totally, and the hairs themselves occasionally differentiated into several types in terms of length, curvature, colour and basal insertion. The development of the pockets bent the U-shaped St8 in the dorso-ventral plane, resulting in a thin strap supporting the edge of the pockets ventrally, termed the anterior arm of St8, and two thin bars projecting posteriorly above the opening of the pockets, the lateral arms of St8. The membrane between the lateral arms can be variously scaled.

In the Argyrogrammatini, the lateral arms of St8 are further modified. Initially, they develop apical secondary hair brushes. In some genera, the lateral arms also develop sub-basal, exterior lobes, which represent the attachment points of the secondary hair brushes. The part of the lateral arm that is distal to this lobe is referred to as the dorsal arm of St8, as it is a morphologically recognizable subdivision of the lateral arm that lies dorsal to the hair pencils. In some argyrogrammatines, the dorsal arms bear flat plates of greasy, closely appressed scales.

As alluded to above, many *Chrysodeixis* species have even more modified structures on A8. *C. argentifera* is unmodified and is thus interpreted as being a relatively plesiomorphic species in terms of

these structures. In other species, however, and especially *C. chalcites* and *C. kebea*, the sternal hair pencils have been lost entirely and St8 modified into a compact sagittate sclerite (Fig. 250). The function of the sternal hair pencils has been taken over by the secondary hair brushes, which have moved ventrally and become retracted into a shallow, semi-circular pocket. T8 has also become highly modified into a U-shaped sclerite with thin arms. It also has attenuated lateral and anterior arms that enclose and support the pocket of the secondary hair brushes (Figs 251–253). In consequence, T8 in the 'higher' *Chrysodeixis* has become remarkably convergent in form upon St8 in other argyrogrammatines, except that its components are rotated through 180 degrees relative to those of St8.

The sternal hair pencils and associated structures of *Trichoplusia ni* have been described in detail by Grant (1971) and their role in courtship was explained by Gothilf & Shorey (1976).

Tegumen and uncus. In most species examined in this study, there occur, latero-apically on the arms of the tegumen, two small sclerites that project posteriorly and under the base of the uncus. These are termed the 'latero-apical sclerites of the tegumen' or LASTs. They may represent the remains of the gnathos since they occur 'ventro-laterad of the articulation of the uncus and socii if present' (Tuxen, 1970).

Vinculum and pleurite. In this study, most of the species examined lacked a saccus in the male genitalia as commonly understood. Instead, the arms of the vinculum converge to a point. In several genera, dorsal and ventral flanges of these arms are produced and fused to form saccus-like structures but are referred to by their appearance rather than as sacci.

The pleurite (termed the paratergal sclerite by Tikhominov, 1979) is a small sclerite, often curved and flanged, that is found exteriorly and laterally at the point where the vinculum and tegumen arms meet. In a few genera, the pleurite was seen to be continuous basally with the outer surface of the vinculum and thus appears to be an extension of the latter. In many plusiines, the base of the pleurite has become sharply kinked and may have lost its connection with the vinculum. In a small number of taxa, the pleurite has become fused with the dorsal edge of the tegumen or may have been lost altogether. In several genera, the vinculum arms continue posterior to the origins of the pleurites and these extensions are termed the ventral, apical, vinculum bars (VAVBs).

Valve. There is much confusion and ambiguity concerning the terminology of the valves and their constituent structures. In this study, the following terminology is adopted. The valves are the paired, presumably clasping organs of the male genitalia. The dorsal edge of the valve is the costa; the ventral, often recurved edge, the sacculus. At the base of the sacculus is produced a usually tubular appendage termed the clavus, while more distally, a similar structure is termed the harpe. The harpes are much more variable in form than the clavi. The transtillae are sclerotized bars, produced from the bases of the costae, that project inwards and support the anellar membrane dorsal to the aedeagus. The aedeagus is supported ventrally by the juxta.

Aedeagus. The muscular tube arising from the base of the aedeagus, down which the spermatophore passes, is termed the cuticular simplex (Callahan, 1960). If present, the enlarged section of the aedeagus basal to the origin of the cuticular simplex, especially if bulbous, is termed the coecum. References in the character descriptions of structures on the vesica as LHS (left hand side) and RHS (right hand side) are from the moth's point of view.

Female A1–7. All of the taxa examined in this study, in common with the majority of the rest of the Noctuoidea, possess a counter-tympanal hood. This takes the form of a rounded, quadrate, sclerotized flap produced from the pleural region of segment A2. It is concave on its inner surface and curves forward to protect the metathoracic tympanal organ. The Euteliinae, Stictopterinae and Plusiinae were observed to possess a second hood-like structure, antero-ventral of the counter-tympanal hood, which is often referred to in the literature as a 'secondary tympanal hood'. Close examination, however, shows that it is a flattened pouch, the two walls of which are separate (Figs 230–231), not a single, solid structure, as is the counter-tympanal hood. I will therefore refer to it as the 'pleural pouch'.

The inner and outer surfaces of the pleural pouch are supported by two separate sclerotized bars of markedly different origins. A latero-apical production of the outer margin of the anterior apodeme of St2 (Figs 230–231) projects antero-laterally and then recurves sharply postero-ventrally to support the inner surface of the pouch. In contrast, the outer surface of the pouch is supported by a ventro-anterior extension of the post-spiracular bar (Fig. 231).

In most euteliines, stictopterines and plusiines examined, the pleural pouch is a large structure, projecting antero-ventrally below the counter-tympanal hood. However, in *Polychrysia* and its relatives

(see character 178), the pouch is small and has moved dorsally so as to be partially concealed by the counter-tympanal hood (Fig. 232).

Female genitalia. The correct homologies of segment 8 of the female noctuid have yet to be fully elucidated. For the purposes of this work, T8 will refer to the sclerotized semi-annulus encircling A8 dorsally and laterally. The often membranous section between the edges of T8 ventrally is termed the lamella postvaginalis (LPV). The antrum is the initial differentiated section of the ductus bursae immediately internal to the ostium bursae. It is frequently more heavily sclerotized and usually much expanded relative to the rest of the ductus bursae. In general, the apex of the corpus bursae is the posteriorly-directed section posterior to the entry point of the ductus bursae into the corpus bursae. The fundus is the opposite, anterior end of the corpus bursae (but see also character 209).

Methods

For each species (except *Plusiotricha, Eutheiaplusia, Stigmoplusia, Chrysanympha, Adeva* and *Loboplusia*), two specimens, one male and one female, were selected. First, general facies and pattern characters were scored from the intact animals. Then, the right fore and hindwings were detached, bleached and mounted in Euparal. From these, the wing structure characters were scored. Next, the head, prothorax, patagia, tegulae and legs were removed, heated in 10% KOH solution, descaled and, except for the head capsule and prothorax, mounted in Euparal. Most characters from these parts were scored before mounting but several required confirmation by observation using a phase contrast compound microscope at ×400. Finally, the abdomens were removed, heated in 10% KOH solution and descaled, particular care being taken with the males not to dislodge the hairs of the subdorsal scent patches or sternal hair pencils, if present. As it was found that many genitalic characters would be obscured and/or distorted by the process of mounting, they were scored from unmounted preparations and routinely checked by dissection of a second example of each sex (except for *Omorphina* for which there was insufficient material). This was not done for the other characters. However, in any instance where there was doubt or ambiguity as to the correct coding of character states, additional specimens were examined. The numbers of each sex of each species studied are given in Appendix 1.

The method varied slightly for the six genera mentioned above, for which only very limited material (2–6 specimens in total) was available. For five genera (not *Loboplusia*), the head and prothorax were not removed. Only one tegula, patagium and set of legs were detached for examination. The wing venation and structure characters were scored by wetting the wing *in situ* with ethyl acetate. The female frenulum was examined by carefully brushing the scales away at the base of the wing underneath with a 00 sable-hair brush. The genitalia of one male and one female only were dissected. For *Loboplusia*, only one set of legs was removed from the paratype male for examination and the genitalic characters were scored from pre-existing slide preparations. These measures resulted in numerous 'missing data' scores (*) in the data matrix. In order to reduce their number and to speed up the computer analysis, any * character that was found to be constant for all the other plusiine taxa was scored appropriately for the six rare genera. These characters were mainly from the head, prothorax, patagia and tegulae. In addition, no females of any of the three species of *Plusiotricha* (*P. livida, P. carcassoni* Dufay and *P. fletcheri* Dufay) are known and thus characters 14, 176, 177 and 179–216 were scored as *. Character 178, scored from females in all other genera, was scored from the male in *Plusiotricha*. Several characters also exhibited dependency upon the possession of certain states for other characters. These non-comparable characters were also scored as *. The data matrix is presented in Appendix 3.

Scanning electron micrographs of proboscis structures were obtained using samples heated in 10% KOH solution, air-dried, affixed to stubs using an epoxy resin, coated with gold for 90s using a sputter coater (Polaron E5000), and then observed using a Cambridge S180 scanning electron microscope, with an accelerating voltage of 10 kV.

Characters

Where possible, the states of a character were arranged into an ordered transformation series. The states of such a series are coded 0 (plesiomorphic), 1, 2 . . . n (most apomorphic). For a number of characters, there was uncertainty as to the most appropriate ordering of the states. These characters are analysed as unordered (using the UNORDERED option of the PAUP program; see also Analytical procedure), wherein no *a priori* assumptions of the order of state transformations is made. Unordered characters are indicated below by an asterisk and the coding of their states 0, 1, 2 . . . n carries no connotation of polarity or transformation sequence.

In several of the descriptions, the symbol ± is used to signify 'more or less' or 'approximately'. Scale lines on the figures are all 1 mm unless otherwise stated.

Wing pattern

1 *Raised scales in the forewing cell absent* **(0)**/*present* **(1)**.

2 *Orbicular, suborbicular and reniform stigmata outlined in black, the former two partially or totally fused* (Figs 32, 33) **(1)**/*stigmata not so formed* **(0)**.

3 *Lower half of suborbicular stigma, with or without a basal, exterior spot, modified to form a Y-mark* (e.g. Figs 39, 43, 87) **(1)**/*not* **(0)**.

4 **Forewing colour internal to the terminal line not pink* **(0)**/*varying from a few scattered pink scales to a distinct pink line* **(1)**/*a pink line tending to be concentrated at the apex of vein* M_3 (Fig. 53) **(2)**/*a conspicuous pink spot at the apex of vein* M_3 (Fig. 54) **(3)**/*a distinct white line* **(4)**.

5 *Single black scales scattered over the wing surface* (Figs 62, 71) **(1)**/*not* **(0)**.

6 *Scale tooth on the forewing tornus well developed* (Figs 46, 86) **(1)**/*weakly developed or absent* (Figs 90, 92) **(0)**.

7 *Basal two-thirds of hindwing yellow* **(1)**/*grey or brown* **(0)**.

8 *Base of hindwing upperside with broad scales* **(0)**/*hindwing base hyaline, scales setaceous* (Figs 98, 99) **(1)**.

9 *Forewing with large, discrete patches of green-gold metallic scales* (Figs 47, 84, 85, 102) **(1)**/*not* **(0)**.

10 *Forewing with metallic sheen over parts, not arranged into discrete patches* **(1)**/*forewing without metallic sheen* **(0)**.

11 *Forewing with a conspicuous black spot in fringe at apex of* M_3 (Figs 38, 39, 51) **(1)**/*not* **(0)**.

12 *Reniform stigma at least partially outlined in silver* (Figs 58, 79, 92) **(1)**/*not* **(0)**.

13 *Forewing cell underside with hair-like scales* **(1)**/*without such scales* **(0)**.

Wing structure

14 **Structure of female frenulum:*

(0): *1 < (2 = 3); 1 finer and just shorter than 2 and 3* (Fig. 124);
(1): *1 < (2 = 3); 1 is finer and half the length of 2 and 3* (Fig. 125);
(2): *1 < (2 = 3); 1 is very fine and almost lost* (Fig. 126);
(3): *1 < 2 < 3* (Fig. 120);
(4): *2 < 3; 1 lost* (Fig. 121);
(5): *3 only; 1 and 2 lost* (Fig. 122);
(6): *1 = 2 = 3 = 4; 4 setae present* (Fig. 123).

A single specimen of *Pseudeva* was observed with four setae on the right wing only, while a single *Omorphina* was observed with five setae on each wing. All other examples of these genera examined showed state 0.

15 *Hindwing vein* M_2 *as strong as* M_3 (Fig. 131) **(0)**/*half the width of* M_3 (Fig. 132) **(1)**/*vestigial (no trachea visible internally)* (Fig. 133) **(2)**/*lost completely* (Fig. 134) **(3)**.

16 *Apex of forewing vein* R_4 *produced as a point beyond the apex of* R_5 *and* M_1 (Fig. 129) **(1)**/*not* (Fig. 130) **(0)**.

17 *Forewing vein* R_{2+3+4} *(upper edge of the areole) approximately parallel to* R_1 (Fig. 135) **(0)**/*markedly converging on* R_1 *then curving away distally* (Fig. 136) **(1)**.

18 *Hindwing vein* M_2 *arises near* M_3 *such that* $M_2 - M_3 \leq M_3 - CuA_1$ (Fig. 134) **(0)**/M_2 *arises less than halfway between* M_3 *and the bend in* $m_1 - m_3$, $M_2 - M_3 >> M_3 - CuA_1$ (Fig. 137) **(1)**/M_2 *arises half way between* M_3 *and the bend in* $m_1 - m_3$, $M_2 - M_3 >> M_3 - CuA_1$ (Fig. 138) **(2)**/M_2 *arises at the bend in* $m_1 - m_3$, $M_2 - M_3 >>> M_3 - CuA_1$ (Fig. 139) **(3)**.

19 *Hindwing vein* M_2 *apex produced as a blunt point, giving five concavities between* R_s *and* CuA_2 (Fig. 128) **(0)**/M_2 *apex not produced, giving four concavities* (Fig. 127) **(1)**.

20 **Scale bases on wings randomly distributed* (Fig. 140) **(0)**/*arranged in irregular transverse rows between the veins* (Fig. 141) **(1)**/*arranged in highly regular transverse rows, one scale wide* (Fig. 142) **(2)**. This character is scored by observation of the scale base arrangement between forewing veins M_3 and M_4.

21 *Forewing vein CuP absent* **(0)**/*a distal short length of vein CuP present* (Fig. 143) **(1)**.

Head

22 *Scales anterior to the bases of the antennae unmodified* **(0)**/*modified into lashes, not exceeding the eye diameter* **(1)**/*lashes exceeding the eye diameter* **(2)**.

23 *Eyes large and bulbous* (Figs 95, 152) **(1)**/*not* (Figs 88, 148) **(0)**.
24 *Prominent rim round eye absent* (Fig. 148) **(0)**/*present* (Fig. 151) **(1)**.
25 *Lower frons scaled only at the edge* **(1)**/*narrow, central band of frons, at most, unscaled* **(0)**.
26 *In lateral view, frons distinctly exceeding the eye* (Figs 147, 148) **(0)**/*frons barely exceeding the eye, if at all* (Figs 149, 150) **(1)**.
27 **Pilifers elongate* (Fig. 144) **(0)**/*triangular* (Fig. 145) **(1)**/*very broadly triangular, not exceeding the labrum* (Fig. 146) **(2)**.
28 *Ventral to antennal sockets, frons slightly concave, so giving the appearance, in front view, of a dorsally delimited frons* (Fig. 147) **(0)**/*no such concavity, frons appearing undelimited ventral to the antennal sockets, sockets contiguous with it* (Fig. 149) **(1)**.
29 *Postocciput flat or slightly concave* (Fig. 149) **(0)**/*distinctly convex and bulged* (Fig. 147) **(1)**.
30 *In the male, frons approximately square, as long as wide* (Fig. 151) **(0)**/*distinctly narrower than long* (Fig. 152) **(1)**.

Proboscis

31 **Proboscis distally armed with no styloconic sensilla* **(0)**/*few* (Fig. 108) **(1)**/*many* (Fig. 109) **(2)**.
32 **Proboscis long and thin* **(0)**/*shorter and stouter* **(1)**/*reduced and non-functional* **(2)**.
33 *Styloconic sensilla with segment 1 cylindrical* (Figs 110, 111) **(0)**/*with five longitudinal ridges, apically produced to give a stellate appearance when viewed end-on* (Figs 112, 113) **(1)**/*with the three distal ridges produced as 'wings'* (Figs 114, 115, 116) **(2)**.
34 **Setae on outer surface of proboscis restricted to approximately the most basal half turn* **(0)**/*continuing almost to the tip and the section with dense styloconic sensilla* **(1)**/*continuing to the apex* **(2)**.
35 **Strengthening bars of proboscis in the most apical part semi-circular* (Fig. 108) **(0)**/*broken up into small, individual nodules* (Fig. 117) **(1)**/*as (1) but nodules only at the extreme apex* (Figs. 109, 118) **(2)**. A nodular apex (state 1) is also found in many butterflies (Sellier, 1975) and probably represents the plesiomorphic condition.
36 *Basal microspines on proboscis irregularly and sparsely distributed* **(0)**/*arranged in regular, dense, circumferential rows* (Fig. 119) **(1)**.

Labial palps

37 *Ventral edge of segments 1 and 2 fringed with hairs* **(0)**/*fringed with broad scales giving a smooth edge* **(1)**.
38 *Lateral scales of segment 2 adpressed* **(0)**/*semi-erect* **(1)**.
39 *Ventral fringe of segment 2 (and usually 3) formed into a neat ridge, giving a blade-like appearance* **(1)**/*scales loose, edge not blade-like* **(0)**.
40 *Segment 1 more than two-thirds length segment 2* (Fig. 155) **(0)**/*segment 1 approximately equal in length to segment 2 or slightly longer* (Fig. 153) **(1)**.
41 *Segment 3 approximately as long as segment 2* (Fig. 156) **(1)**/*segment 3 only two-thirds as long as segment 2 or less* (Fig. 155) **(0)**.
42 *Apex of segment 3 blunt* (Fig. 155) **(0)**/*acutely pointed* (Fig. 154) **(1)**.
43 *Vom Rath's organ conspicuously papillate basally* (Fig. 158) **(1)**/*not* (Fig. 159) **(0)**. All VROs are papillate in that they have individual internal invaginations, presumably housing sensilla. However, regular papillations, clearly visible under ×10 magnification, are termed conspicuous.
44 *Segment 3 much longer than wide* (Fig. 155) **(0)**/*subspherical* (Fig. 153) **(1)**.

Antennae

45 *Ventral hairs on male antenna short, less than width of the segments* (Fig. 162) **(0)**/*long and apically very flexuous, much longer than segments are wide* (Fig. 161) **(1)**.
46 **Male antennae simple* (Figs 43, 162) **(0)**/*asymmetrically bipectinate* (Figs 100, 161) **(1)**/*symmetrically bipectinate* (Figs 92, 160, 163) **(2)**.
47 **Pectinations of male antenna apically with a single small seta* (Fig. 161) **(0)**/*with a single large, stout seta* (Fig. 160) **(1)**/*with two apical setae* (Fig. 163) **(2)**.
48 *Longest pectinations on male antennae arising from base of the segments* (Fig. 163) **(0)**/*arising distally on the segments* (Figs 160, 161) **(1)**.

External structure of thorax – scaling, patagia, tegulae

49 *Large, bilobed, truncate crest present on TII* (Fig. 39) **(1)**/*absent* (Fig. 104) **(0)**.

50 *Tegulae adpressed to TII* (Fig. 72) **(0)**/*tegulae held almost vertically away from TII* (Fig. 62) **(1)**.
51 *Dorsal arm of tegula bluntly pointed or rounded* (Fig. 166) **(0)**/*truncate* (Fig. 164) **(1)**.
52 **Ventral arm of tegula bluntly pointed* (Fig. 171) **(0)**/*truncate* (Fig. 172) **(1)**/*spatulate* (Fig. 173) **(2)**.
53 *Ventral arm of tegula with a colourless, microspinose extension* (Fig. 169) **(1)**/*not* (Figs 168, 170) **(0)**.
54 *Microspines on ventral tegula arm restricted to apex and outer edge* (Figs 168, 169) **(0)**/*microspines extending along inner edge towards main body* (Fig. 170) **(1)**.
55 *Ventral arm of tegula produced on a lateral extension of the main body, outer edge of dorsal arm almost evenly continuous with the dorsal surface of the ventral arm* (Figs 165, 167) **(1)**/*ventral arm not on a lateral extension, outer edge of dorsal arm curves back dorsally to form a distinct ridge running roughly parallel to the outer edge of the ventral arm* (Figs 164, 166) **(0)**.
56 *Dorsal tegula arm with a broad marginal flange* (Fig. 174) **(1)**/*flange very narrow (less than 1 scale base wide) or absent* (Fig. 175) **(0)**.
57 *Attachment point of patagium drawn out* (Fig. 176) **(1)**/*not* (Fig. 177) **(0)**.

Legs

58 *Foretibia with a dorsal white spot* (Fig. 87) **(1)**/*without such a spot* (Fig. 84) **(0)**.
59 *Hind tibia and tarsi transversely banded grey, black or brown and white dorsally* (Fig. 44) **(0)**/*dorsally unicolorous white, pale grey or pale orange* (Figs 34, 87) **(1)**.
60 **Basitarsal comb on male hindleg absent* (Fig. 178) **(0)**/*present as a single row of short setae (approximately equal to the width of the basitarsus or to the length of the SV spines)* (Fig. 179) **(1)**/*a single row of long, fine setae (approximately 2× the width of the basitarsus or the length of the SV spines)* (Fig. 180) **(2)**/*as (2) but setae in multiple rows* (Fig. 181) **(3)**.
61 *Inner row of SV spines on the fore-tarsi present in male on all segments along the entire length of each* **(0)**/*inner row ± suppressed over basitarsus (apical and subapical spines may remain)* (Fig. 182) **(1)**/*inner row ± suppressed on all segments, outer row suppressed on tarsi 2–5* (Fig. 183) **(2)**/*all SV rows suppressed, V row of spines on basitarsus short and stout* (Fig. 184) **(3)**.
62 *Spines of hindbasitarsal SV and V rows equal along segment in both sexes* (Fig. 185) **(0)**/*spines on basal half of segment smaller and finer* (Fig. 186) **(1)**/*spines suppressed on basal half of segment* (Fig. 187) **(2)**. For the purposes of coding character 62, the male hindbasitarsal comb of certain plusiines has been ignored.
63 **Fore- and midtibiae unspined* **(0)**/*with 1–2 apical spines on outer surface (occasionally 1 on foretibial inner surface)* (Fig. 195) **(1)**/*fore- and midtibiae extensively spined on both surfaces* (Fig. 196) **(2)**.
64 **Hindtibiae unspined* **(0)**/*spined on outer surface distal to median spur insertions* (Fig. 188) **(1)**/*spined along entire outer surface* (Fig. 189) **(2)**/*spined between the median and apical spur insertions subventrally on inner surface* (Fig. 190) **(3)**.
65 **Tarsi with few small, SD and D setae* (Fig. 194) **(0)**/*with a small number of additional large spines, of the same form as the SV and V spines* (Fig. 193) **(1)**/*with a few SD and D setae, finer than the SV and V rows* (Fig. 192) **(2)**/*with numerous long, fine SD and D setae* (Fig. 191) **(3)**.
66 *Hindleg (measured as femur base to apex of pretarsus) subequal to midleg or longer* **(0)**/*hindleg shorter than midleg by approximately half the length of the mid-femur* **(1)**.
67 *Claw with a ventral lobe* (Figs 201, 202, 203) **(1)**/*claw evenly curved ventrally* (Fig. 204) **(0)**.
68 *Hindleg inner apical spurs less than half the length of the basitarsus* (Figs 199, 200) **(0)**/*approximately three-quarters length of the basitarsus, occasionally subequal to it* (Fig. 198) **(1)**/*spurs as long as basitarsus or longer* (Fig. 197) **(2)**.
69 *Foretibia with a dorso-apical claw* (Figs 205, 206, 207) **(1)**/*claw absent* **(0)**.

Internal structure of prothorax

70 *Dorsal arms of furca vertical, not apically produced* (Fig. 209) **(0)**/*dorsal arms produced and curved posteriorly* (Fig. 210) **(1)**.
71 *Dorsal edge of epimeron with a dorso-ventral ridge running from near the dorsal furcal arms to the apex of the SV furcal arms* (Figs 212, 213) **(1)**/*without such a structure* (Fig. 211) **(0)**.

Male abdomen A1–7

72 *Abdomen cylindrical or broadly tapered* **(0)**/*abdomen distinctly narrowly tapered, A7 half the width of A2* **(1)**.
73 **Internal flange on anterior edge of T2 curved and of uniform diameter* (Figs 216, 219) **(0)**/*with two SD lobes* (Fig. 220) **(1)**/*lobes almost fused but with a central emargination* (Fig. 221) **(2)**/*flange semicircular, ventral edge straight* (Figs 217, 218) **(3)**. The flange in *Cucullia* is broad but uniformly so and with a

distinctly concave ventral edge thus distinguishing it from state 3 in which the ventral edge is straight. The flange in *Lophoptera* is reduced but still has a straight ventral edge, as well as the characteristic triangular dorsal inflection. The latter structure also serves to distinguish state 3 from extreme forms of states 0 and 2.

74 *Central membranous area of St2 flanked by grooves arising from anterior apophyses or by flat cuticle* (Fig. 222) **(0)**/*flanked by two internal longitudinal flanges arising from the bases of the anterior apophyses, and which are directed obliquely towards the midline* (Fig. 223) **(1)**.

75 **All components of trifine basal abdominal hair pencils absent* **(0)**/*some components present* **(1)**/*all components present* **(2)**. Of the five main components of the trifine hair pencils (Birch, 1972*a*), *Magusa* possesses only the lever and the pockets, and these are reduced and non-functional. Because this condition could be the result of partial gain or loss, the character is treated as unordered.

76 *St7 broad, ± entire* (Fig. 208) **(0)**/*St7 with two postero-lateral sclerotizations, giving a 'fish-tail' appearance* (Figs 214, 215) **(1)**.

77 *Dorsal-lateral hair tufts on A2–7 absent* **(0)**/*present on A5–7* (Figs 46, 57) **(1)**/*additional 'secretory' areas present on A4, occasionally on A2–3* **(2)**/*distinct additional tufts present on A4* **(3)**. The secretory areas on A2–4 are very friable and are easily lost during preparation. Thus no attempt was made to subdivide state 2, especially as it would not be possible to reliably score *Eutheiaplusia* and *Plusiopalpa*. *Loboplusia* has a unique distribution of what may be the scale bases of scent tufts on the pleura of A2–4 but this is uncertain from the descaled preparation. The genus was thus coded as *.

78 **Scent hairs on A7 exposed* (Fig. 226) **(0)**/*enclosed in an invaginated groove* (Fig. 227) **(1)**/*enclosed in an overfold of pleuron 7* (Fig. 228) **(2)**/*enclosed in a membranous fold* (Fig. 229) **(3)**. These three states are probably independent derivations.

79 **Dorso-lateral hair tufts on A5–6 with indistinct edges* **(0)**/*tufts on A5–6 with distinct, sharp antero-medial edges* **(1)**/*as (1) but A5 only* **(2)**/*as (1) but A6 only* **(3)**.

Male St8 and the ventral hair pencils

80 **St8 with a thin anterior bar and two broad lateral bars extending posteriorly* (Fig. 235) **(0)**/*lateral bars of St8 thin* (Fig. 243) **(1)**/*as (1) but anterior bar narrowed medially, often with latero-ventral, posteriorly-directed sclerotized flaps* (Fig. 254) **(2)**/*lateral arm of St8 produced at an acute angle to the anterior arm* (Figs 236–240) **(3)**. This character probably comprises two independently derived forms of St8 and hair pencil: the plusiine type, states 1 and 2; and the stictopterine type, state 3. The plusiine type is probably derived directly from state 0 but this is much less certain for state 3. Subsequently, the two types of hair pencil and associated St8s will be treated as mutually exclusive. Characters applicable to one type will be coded in taxa showing the other type as *. The same coding will be used for those taxa showing state 0 for 80. Several taxa exhibit partial reductions of the hair pencils and St8. *Cucullia* and *Abrostola* have much reduced lateral arms but still can be interpreted as 80(3) and 80(1) respectively. In the following hair pencil characters, 81–82 refer to the stictopterine type, while 83–95 refer to the plusiine type.

81 **Hair pencils arising from a diamond-shaped pocket posterior to the anterior arm of St8* (Figs 238, 239) **(0)**/*from two shallow ventral pockets* (Fig. 240) **(1)**/*from two deep lateral pockets* (Fig. 237) **(2)**/*pencils reduced to a ventral row of scales arising from a very thin sclerotized bar running just posterior to and parallel with the anterior arm of St8* (Fig. 236) **(3)**. These four forms of hair pencil appear to be mutually exclusive.

82 *Angle formed by anterior and lateral arms of St8 without an exterior lobe* (Fig. 236) **(0)**/*with a small exterior lobe* (Fig. 238) **(1)**/*with a large, dorsally recurved bar* (Fig. 239) **(2)**.

83 **Hair pencils poorly developed, merely a tuft of sparse scales arising from a shallow depression* (Fig. 241) **(0)**/*hair pencil pockets slightly invaginated but still not discrete* (Fig. 245) **(1)**/*pockets well developed, partially fused along their length* (Fig. 243) **(2)**/*pockets well developed, separate along their entire length from St8 to their apices* (Fig. 244) **(3)**/*pockets well developed, totally fused into a single structure but the two individual pencils still discrete* (Fig. 265) **(4)**/*single pocket present, elements fused* (Figs 242, 248) **(5)**. It is uncertain whether the undeveloped hair pencils of *Abrostola* and of *Polychrysia* and its relatives are plesiomorphically undeveloped or the result of subsequent reduction. All these genera were coded 0.

84 *Hair pencil pockets with a sclerotized bar along the inner ventral edge* (Figs 254, 258) **(1)**/*absent* (Figs 256, 263) **(0)**.

85 *Hair pencil insertions in one main apical field* (Figs 255, 262) **(0)**/*hair pencil insertions differentiated with distinct, discrete subdorsal and lateral fields* (Figs 258–260, 269–271) **(1)**.

86 *Hair pencil pockets with small subventral basal accessory pouches* (Figs 260, 263) **(1)**/*absent* (Fig. 257) **(0)**.

87 *Hair pencils composed of scales of one length* (Fig. 257) **(0)**/*outer scales markedly shorter than inner scales* (Figs 263, 264, 267, 268) **(1)**.

88 *Hair pencils with an inner tuft that is much longer than the remaining inner scales of the pencil* (Figs 260, 272, 273) **(1)**/*all inner scales of approximately equal length* (Fig. 266) **(0)**.

89 *Lateral arms of St8 bearing secondary hair brushes* (Figs 242, 261, 267) **(1)**/*not* **(0)**.

90 *Lateral arms of St8 with an anterior flange where they curve dorsally over the hair pencils* (Figs 260, 271) **(1)**/*without such a flange* (Fig. 264) **(0)**.

91 *Lateral arms of St8 undifferentiated, running to posterior margin of segment 8 as uniform linear bars dorsal and lateral to the hair pencils* (Fig. 243) **(0)**/*lateral arms twisted dorsally over the hair pencils* (Fig. 257) **(1)**/*as (1) but also with a deep basal concavity in outline* (Fig. 262) **(2)**.

92 **Lateral arms of St8 roughly linear* (Fig. 244) **(0)**/*with a broad triangular exterior sub-basal lobe* (Fig. 256) **(1)**/*lobe modified into a blunt projection* (Fig. 258) **(2)**/*lobe attenuate and recurved dorsally* (Fig. 265) **(3)**.

93 **Dorsal arms of St8 run parallel and do not meet apically* (Fig. 245) **(0)**/*dorsal arms converge to a point* (Fig. 254) **(1)**/*dorsal arms run approximately parallel, fusing into a rounded apex* (Fig. 263) **(2)**/*dorsal arms run transversely, approximately at right angles to the long axis of the body* (Figs 258, 269) **(3)**. The dorsal arms are missing in *Eutheiaplusia*, the genus being coded * for those characters (93–94) dependent upon their presence.

94 **Ventrally, dorsal arms of St8 unscaled or with unmodified scaling* **(0)**/*with broad, spatulate, erect scales* (Fig. 242) **(1)**/*with broad, flat, 'greasy-looking' scales, appressed to the surface and adhering into sheets* **(2)**/*with scales as in (2) but those apically on the dorsal arms formed into a semi-circular flat plate projecting distally* (Figs 258, 269) **(3)**.

95 *Membrane between lateral arms of St8 ventrally bare* **(0)**/*covered in long, fine, hair pencil-like scales* **(1)**. These hairs are very easily brushed off, which may be what has happened in the genera *Antoculeora, Macdunnoughia* and *Allagrapha*, in which the hairs are very sparse but nevertheless recognizable.

Male genitalia – uncus, tegumen & anal tube

96 *Uncus a simple, ± cylindrical tube* (Fig. 284) **(0)**/*uncus flattened ventrally so it is D-shaped in cross-section* (Fig. 286) **(1)**/*uncus reduced to a subspherical structure* (Figs 276, 277) **(2)**. This character is treated as unordered. The three types are treated as independent for appropriate subsequent uncus characters, as was done for hair pencils. It should be noted that there are numerous modifications to state 0, some of which are coded below as separate characters.

97 *Uncus basally curved* (Fig. 282) **(0)**/*straight* (Fig. 283) **(1)**. State 0 can show considerable variation (Figs 281, 282, 284, 285).

98 *Uncus of even width or gradually tapering distally* (Fig. 284) **(0)**/*uncus distinctly distally dilated dorsally* (Fig. 293) **(1)**.

99 *In lateral view, dorsal margin of tegumen ± continuous with dorsal margin of uncus* (Fig. 282) **(0)**/*a distinct notch present between tegumen and uncus* (Fig. 285) **(1)**/*apex of tegumen produced, apical angle about 90 degrees* (Fig. 287) **(2)**. In state 1, the notch is formed by the downcurvature of the apex of the tegumen and the increased basal curvature of the uncus. In state 2, the tegumen curvature is accentuated to a sharp angle. *Abrostola* is superficially state 2 but the tegumen is apically rounded (see Fig. 274). State 0 may be flat or have a uniform convex curve (Figs 281, 284). Several plusiines (e.g. *Trichoplusia, Dactyloplusia* and *Palaeographa*) have a reduced state 1 that superficially looks like state 0.

100 *Base of uncus convex* (Fig. 285) **(0)**/*concave* (Figs 274, 279) **(1)**.

101 *In lateral view, dorsal edge of tegumen, distal to pleurite, evenly curved or straight, with at most a short, flat apex* (Fig. 281) **(0)**/*with a distinct angle, just over halfway along; when origin of uncus is horizontal, the distal section of tegumen dips towards uncus base* (Fig. 285) **(1)**. Many other genera have flat distal sections to the tegumen (e.g. *Diachrysia, Chrysodeixis, Palaeographa*) but these are all horizontal when the uncus base is aligned as described above.

102 *Uncus medially cylindrical* **(0)**/*medially slightly to greatly dorso-ventrally flattened and laterally expanded* (Figs 275, 278) **(1)**.

103 *In dorsal view, uncus with a distinct median suture visible, especially basally* (Figs 275, 278) **(1)**/*absent* (Figs 288, 290) **(0)**.

104 *In dorsal view, outer edges of tegumen diverge at about 90 degrees or less* (Figs 288, 290, 296) **(0)**/*outer edges diverge at almost 180 degrees* (Figs 295, 297) **(1)**.

105 *Dorsal edge of anal tube arising from base of uncus or extreme apex of tegumen* (Fig. 282) **(0)**/*anal tube*

arising from bases of latero-apical sclerites of the tegumen (LASTs) to about halfway along the LASTs, free of uncus base (Fig. 284) **(1)**.

106 *LASTs free apically of ventral edge of tegumen, projecting to articulate with the uncus base* (Fig. 275) **(0)**/*LASTs fused to underside of tegumen, ± fused dorsally around uncus base* (Figs 290, 296) **(1)**. Also, in *Paectes*, the LASTs extend ventrally under and fuse under the anal tube as a sharply pointed structure, a true gnathos. In their reduced form, the plesiomorphic state consists of a pair of lateral bars extending from the ventral margin of the tegumen to the uncus base. In the plusias, the membranous portion becomes sclerotized, either completely or leaving only a small, circular membranous area basal to the uncus medially. In some weakly sclerotized genera (especially *Polychrysia* and its relatives), there may be subsequent desclerotization but this is general and the plesiomorphic condition is not displayed. *Plusiopalpa dichora* has extensive membranous areas centrally but overall is like the other plusias. LASTs are absent in *Anuga*.

107 *Dorsal surface of anal tube membranous* **(0)**/*with two subdorsal bars arising from the LASTs* **(1)**. These bars are very weak in *Abrostola*. In *Stictoptera, Lophoplusia, Lophoptera* and *Chrysanympha*, the connection with the LASTs is tenuous, while the bars in the latter two genera are fused into a single dorsal bar. The bars in *Mouralia* bear subdorsal, wing-like projections.

Male genitalia – vinculum & pleurite

108 *Vinculum arms with a small, distinct, ventral tooth* (Fig. 303) **(1)**/*without a tooth* (Fig. 308) **(0)**.

109 *In lateral view, vinculum apically straight or with only a single slight curve* (Fig. 299) **(0)**/*vinculum with two apical curves, dorsally then ventrally* (Fig. 319) **(1)**.

110 *Arms of vinculum ± straight in ventral view, vinculum V-shaped* (Fig. 303) **(0)**/*arms bent about halfway along, vinculum Y-shaped* (Fig. 301) **(1)**. State 1 shows a distinct Y-shape, with the anterior parts of the vinculum arms running ± parallel. In *Polychrysia* and several other genera, the vinculum is slightly Y-shaped but the distal parts still markedly converge.

111 *Vinculum apically produced as a long, thin spine* (Figs 300, 308) **(1)**/*vinculum not so produced* **(0)**. Both *Pseudoplusia* and *Chrysodeixis* have vincula produced to a sharp point. In *Stigmoplusia*, the vinculum apex is rounded.

112 **Dorsally and subapically, dorsal flanges of the vinculum arms with even edges* (Fig. 303) **(0)**/*edges with two small emarginations towards the exterior* (Fig. 298) **(1)**/*emarginations produced into two sharp points* (Figs 299, 300) **(2)**/*emarginations produced into two blunt posteriorly-directed hooks* (Figs 304, 305) **(3)**.

113 *Dorsal and ventral flanges of vinculum arms greatly expanded and flattened dorso-ventrally forming a broad flat cone, unfused medially, sides of vinculum subparallel* **(1)**/*flanges of vinculum arms not so enlarged* **(0)**. The apomorphic state for this character is a complex one that has to be qualified. The subparallel sides are also found in those genera exhibiting state 1 of 110 but they do not have expanded and flattened flanges. In *Lophoptera* (Fig. 309), the flanges are expanded and flattened, but they are medially fused to form a complete cone and the edges are distinctly convergent.

114 *Dorsal and ventral flanges of vinculum arms separate or, at most, ventral flanges fused* **(0)**/*dorsal and ventral flanges fused across to give the appearance of a flattened cone* (Figs 302, 309, 310) **(1)**. In *Eosphoropteryx*, the ventral flanges only are fused across. In *Diloba*, the dorsal flanges may be fused but the general desclerotization makes this difficult to discern. The vinculum of *Stictoptera* is highly derivative and although what is left of the flanges appear to be fused, a complete conical structure is not found and the condition is not strictly comparable. *Stictoptera* was scored *. The fusion in *Paectes* is drawn out but a conical form is still discernible.

115 *Vinculum arms divergent to the base of the tegumen* (Fig. 303) **(0)**/*arms divergent and then run parallel towards, or converge towards, the tegumen* (Fig. 310) **(1)**.

116 *Pleurite dorsally simply concave, ventrally entire or with a desclerotized nick* (Figs 317, 318) **(0)**/*pleurite dorsally strongly concave basally and then with a sharp convex bend caused by a distinct sharp ventral basal notch* (Fig. 312) **(1)**. In *Chalcopasta* and *Oncocnemis*, there is a ventral basal desclerotization but this is not manifested dorsally by a sharp bend. In *Omorphina*, there is a dorso-basal bump but no ventral notch.

117 *Pleurite without a lateral flange, lateral margin somewhat recurved towards the midline* (Fig. 306) **(0)**/*pleurite with a lateral, often broad, flange, lateral margin flat* (Figs 311, 319) **(1)**. In *Anagrapha* and *Palaeographa*, the lateral flange is somewhat reduced in width but the margin is nevertheless flat. *Pseudoplusia* and *Chrysodeixis* have very thin pleurites with no lateral flange (or one that is very narrow). The pleurite of *Anuga* is reduced to a small triangular lobe. In *Paectes*, a pleurite-like flange is fused onto the antero-dorsal margin of the tegumen (see character 123), while in *Diloba*, a thin sclerite, presumably the pleurite, occupies a similar fused position. In the stictopterines, the pleurite

is either reduced to a small lobe (*Stictoptera*) or lost (*Lophoptera*), or fused with the tegumen and the vinculum connection lost.

118 *Apex of pleurite recurved dorsally over the tegumen to articulate on the inner edge in a pocket* (Fig. 314) **(0)**/*pleurite apically lying dorsally on the tegumen or slightly recurved over the inner edge, but not articulating in a pocket* (Fig. 313) **(1)**/*tegumen rotated almost vertically, pleurite apex only in contact with the tegumen, otherwise lying parallel with the ventral apical vinculum bar (VAVB)* (Fig. 316) **(2)**. In state 2, the pleurite and the VAVB appear as linear continuations of the vinculum apex.

119 *Pleurite and VAVB fused basally* (Fig. 312) **(0)**/*fused to about half the length of the pleurite* (Figs 306, 307) **(1)**.

120 *Pleurite broad, curved in lateral view and separate from the antero-dorsal margin of the tegumen* (Fig. 312) **(0)**/*pleurite very narrow, very closely appressed to (but not fused with) the antero-dorsal margin of the tegumen* (Fig. 289) **(1)**.

121 **VAVB a long linear bar projecting from the apex of the vinculum to articulate ventro-apically on the tegumen, apex of vinculum and base of tegumen distinctly separate* (Fig. 312) **(0)**/*VAVB very short or absent, tegumen and vinculum closely approximated* (Fig. 311) **(1)**/*VAVB absent or reduced to a blunt lobe, tegumen and vinculum separated* (Figs 318, 321) **(2)**/*VAVB absent, tegumen produced basally below pleurite to approach vinculum apex* (Figs 315, 317) **(3)**. In state 1, if the VAVB is present, then it is bent, thus allowing the vinculum and tegumen to come into close proximity; in state 0, the VAVB is straight.

122 *VAVB produced ventro-posteriorly into a large, articulated socius* (Figs 291, 292) **(1)**/*not* **(0)**. In *Paectes*, the socii are hairy, unsclerotized, blunt lobes; in *Anuga*, they are long, sclerotized, curved and apically hooked, and are remarkably convergent in appearance upon the typical plusia uncus.

123 *Vinculum and tegumen separate or linked by the VAVB* **(0)**/*vinculum and tegumen broadly joined, pleurite totally fused along the antero-dorsal edge of the tegumen* (Fig. 320) **(1)**. This character could also be represented as yet another alternative state of character 121. However, given that the euteliines and stictopterines have been tentatively coded for character 121 (as opposed to * for *Diloba*), characters 121 and 123 have been retained as separate.

Juxta & anellus

124 *Anellar membrane present between ventral margin of aedeagus and apex of juxta* (Fig. 323) **(0)**/*apex of juxta ± fused to apex of aedeagus ventrally* (Fig. 322) **(1)**.

125 *Apex of juxta uniformly thin* **(0)**/*apex with a transverse apical thickening and a median longitudinal bar* (Figs 324, 325) **(1)**. The longitudinal bar in *Abrostola* is weak, while in *Mouralia*, it is apparently double.

126 *Juxta free from valve latero-basally* **(0)**/*juxta fused to inner edge of sacculus near the base of the clavus by a short thin bar* (Figs 324, 325) **(1)**.

127 *Apex of juxta entire or if decurved, no notch or apical process present* (Figs 325, 329) **(0)**/*apex folded ventrally to form a ± parallel-sided notch that may be partly sclerotized dorsally to form an apical process* (Figs 326, 327) **(1)**/*process well sclerotized distally so as to appear subapical on the juxta* (Figs 335, 336, 340) **(2)**/*process further modified into a sharp upcurving spine* (Figs 337, 338, 339) **(3)**. *Thysanoplusia, Zonoplusia* and *Ctenoplusia* have juxtas in which the apex comes to a point without curving ventrally. Similarly, in *Trichoplusia, Acanthoplusia, Agrapha* and *Anadevidia*, the juxta is apically deeply concave but not decurved. Also, in these six genera, the anellus arises apically from the juxta. In those genera showing states 1–3, the anellus arises dorsally and subapically from the juxta, due to the dorsal sclerotization of the apical process.

128 *Apex of juxta smooth* **(0)**/*apex of juxta scobinate* (Figs 328, 329, 330, 334) **(1)**/*scobinations distally modified into sclerotized thorns* (Fig. 341) **(2)**. The scobinations in *Chrysodeixis* are very weak, while in *Pseudoplusia*, they are restricted to the lateral, distally-produced arms of the juxta. Thus, the states in these two genera may not be homologous with that in *Dactyloplusia* and *Thysanoplusia*. The apices in *Plusiopalpa* and *Cucullia* are also heavily scobinate and even spinose (*Plusiopalpa shisa*), but in these genera the juxta merges gradually into the anellus and so it is difficult to say on which structure the ornamentation is located. Nevertheless, they were both coded 1.

129 *Juxta a ± quadrate sclerite, and usually well sclerotized* **(0)**/*juxta crescent- or boomerang-shaped, poorly sclerotized* (Fig. 333) **(1)**. The juxta of *Polychrysia* and its relatives is poorly sclerotized but distinctly quadrate. *Stictoptera* has a highly autapomorphic juxta and is coded *. The juxtas of *Brachionycha* and *Diloba* are somewhat crescentic but are well-sclerotized.

130 *Juxta basally separate from saccular flanges* (Fig. 342) **(0)**/*juxta basally fused to basal saccular flanges* (Fig. 343) **(1)**. Those genera lacking saccular flanges (see character state 131:0) are coded *.

Valve

131 *Base of sacculus evenly rounded* (Figs 372, 373, 374) **(0)**/*with a basal flange* (Figs 351–355) **(1)**.

132 *Saccular flanges fused across and produced medio-anteriorly into a rounded lobe between the valve bases* (Fig. 343) **(1)**/*flanges not so modified* **(0)**. In most genera with saccular flanges, they are either separate from each other or fused across to form an irregular flat area of sclerotization. In two genera (*Panchrysia* and *Chrysanympha*), however, the flanges are formed medially into a rounded, somewhat dorsally concave lobe, giving, with the valve bases, a regular anterior outline like a rounded M or a two-cycle sine wave.

133 *Ventral edge of valve basally with a single row of enlarged flattened blade-like setae* (Figs 351, 355) **(1)**/*without such setae* **(0)**.

134 *Sacculus, distal to clavus, produced into an irregular spatulate lobe* (Figs 347, 348) **(1)**/*not* **(0)**. This structure has been widely interpreted in the past as the clavus. However, its position (more distal on the sacculus margin than the position occupied by the clavus in other noctuids) and the presence of an obvious clavus in the 'correct' location in *Mouralia* argue that the spatulate lobe is not the clavus but a novel development apomorphic for the Abrostolini.

135 *Apex of valve with a distinct uniseriate corona* (Fig. 349) **(1)**/*absent* **(0)**. The corona is defined here as a distinct marginal series of strong basally-directed spines. In *Calophasia* and *Chalcopasta*, the corona is weak and somewhat submarginal.

136 *Apex of valve not differentially scaled* **(0)**/*with multiple rows of easily detached, basally-directed, setose scales; when removed, scale bases forming a distinct field* (Figs 351–355) **(1)**.

137 *Marginal setae on ventral edge of valve on normal pinacula* (Figs 347–350) **(0)**/*some setae arising from marginal prominences* (Figs 368, 369, 370) **(1)**. The marginal prominences are much larger than normal pinacula and frequently bear two or more setae.

138 *Valve constricted at about two-thirds of the distance base to apex, apical section spatulate* (Figs 354, 355) **(1)**/*valve not constricted* (Figs 379, 382) **(0)**.

139 *Dorsal edge of saccular overfold with a lobe that overlies and obscures the clavus base when the valves are opened flat* (Figs 360, 368, 369, 370) **(1)**/*clavus base, if present, not obscured by sacculus when valves opened flat* (Figs 348, 361) **(0)**.

140 *Ventral edge of valve basally evenly curved* **(0)**/*with a broad, blunt point about one-third from base* (Figs 351, 352) **(1)**.

141 *Sacculus with a broad, triangular spine basal to the origin of the harpe (if present), often further modified* (Figs 370, 376, 378) **(1)**/*absent* **(0)**. This saccular spine is modified into a quadrate lobe in *Erythroplusia* and into a long, serrate, lance-like projection in *Antoculeora*.

142 *Apex of sacculus continuous with ventral margin of valve* **(0)**/*apex produced as a sheet, costa extended ventrally towards it, but not fused with it* (Figs 368, 369, 370) **(1)**/*saccular sheet and costal overfold fused, often modified into a curved hook* (Figs 361, 372, 373, 374, 376) **(2)**. This character is highly problematical given the high degree of structural diversity displayed by the genera that possess it. *Allagrapha* and *Macdunnoughia* exhibit the simplest form in which the apex of the sacculus is extended beyond the ventral margin of the valve as a broad, blade-like sheet. This is modified in *Puriplusia* into an inwardly-curving hook. In *Autoplusia*, a condition similar to that seen in *Puriplusia* is found, in that the apical saccular process is modified to form an inwardly-curving hook. However, in *Autoplusia*, there is a distinct fusion with the costal margin in the formation of the hook that does not appear to occur in *Puriplusia*. *Sclerogenia* is similar to *Autoplusia* but the hook is larger, apically blunt, and is curved ventrally rather than inward, while the ventral edge of the valve is greatly enlarged, giving the hook an apparently subdorsal origin on the valve. The valve of *Antoculeora* is highly autapomorphic and very difficult to homologize with the valves of the other genera. I have chosen to interpret the ventral valve digitations, and in particular the subapical one, as being homologous to the saccular hook of *Autoplusia* and *Sclerogenia*. However, given that the inner margins of the costa and sacculus in *Antoculeora* are completely fused along almost their entire length, a more comprehensive study is required to confirm this and the previous interpretations of this character.

143 **Median edge of sacculus basally unmodified* **(0)**/*produced into a broad, rounded, setose lobe* (Fig. 356) **(1)**/*lobe elongated into a distinct clavus, dorsal and ventral margins of which are basally ± level* (Fig. 357) **(2)**/*dorsal margin much cut back (or ventral section basally elongate) so that clavus appears to be located on a sclerotized peninsula* (Fig. 358) **(3)**.

144 *Clavus a distinct tubular structure, >3× as long as basally wide* (Fig. 360) **(0)**/*clavus a short tubular structure, about as long as basally wide* (Fig. 380) **(1)**/*clavus reduced to no more than a slight setose bump on the end of the peninsula* (Fig. 382) **(2)**. This character and 145 are dependent upon states of character 143. Character 144 is coded * for taxa showing states 0 and 1 for character 143, while character 145 is coded * in

taxa showing states 0, 1 and 2 for character 143. Character 144 is included because it is one of the 'classic' plusiine characters and is the one used by McDunnough (1944) to divide the plusias into three groups of genera. *Cornutiplusia* and *Polychrysia* both have fairly short clavi but still long enough to be coded 0. Similarly, *Euchalcia* and *Lamprotes* are somewhat intermediate between states 1 and 2 but given that some tubular structure can be detected, they were coded 1.

145 *Clavus borne on a short peninsula* (Fig. 358) **(0)**/*clavus borne on a highly elongate, somewhat flattened peninsula that is about as long as the tubular clavus* (Fig. 359) **(1)**. Genera possessing short or very reduced clavi (character 144: 1 & 2) are not strictly comparable and were coded 0, since in these genera the peninsula is not elongated, but is longer than the clavus by virtue of the latter's reduction.

146 *Valve overall blade-shaped, ventral edge ± straight for about two-thirds of its length, then curved up to the apex of the costa to form a blunt or sharp point* (Fig. 381) **(1)**/*apex of valve ± evenly rounded* **(0)**. The shape of the valve coded by state 1 is readily recognized but difficult to describe and delimit briefly. The general impression is of a knife blade; the valve gradually widens from the base, the costa is slightly concave and the ventral margin possesses well-developed, sclerotized setae. In *Cucullia*, the dorsal and ventral edges of the valve are ± parallel and the genus was coded 0. The valves of *Diachrysia chryson* are less blade-like than most genera coded 1, but other species in this genus, notably *D. nadeja*, are as extreme as the autographas. *Anagrapha* is interpreted as state 1, due allowance having been made for the highly modified, excavated apex in this taxon.

147 *Valve ± oval in outline, roughly symmetrical along the midline* (Fig. 350) **(1)**/*valve not oval, asymmetrical along the midline* **(0)**. *Euchalcia variabilis* has a somewhat quadrate valve but is still coded 1. Most other *Euchalcia* species have simple, oval valves (Dufay, 1968). Note that states 1 for characters 146 and 147 are mutually exclusive. Taxa showing state 1 for one character are coded * for the other.

148 *Harpe present* **(1)**/*absent* **(0)**. If the saccular processes *Autoplusia, Sclerogenia* and *Antoculeora* are reinterpreted as harpes, then states 1 and 2 of character 142 are not part of the same transformation series.

149 *Harpe a blunt, tubular process* **(0)**/*harpe modified into a sharply pointed, basally curved hook* (Figs 354, 367, 379, 380, 386) **(1)**. A number of genera have non-tubular harpes (e.g. *Lophoptera, Calophasia, Macdunnoughia*) that are also not of the form of a curved hook (see also character 150). Because they do not show the apomorphic condition of character 149, these genera will be coded 0, even though they do not possess the plesiomorphic condition for this character either. The same rationale applies to the following character also. The hooked harpes of *Syngrapha, Caloplusia* and *Palaeographa* are almost certainly convergent upon those of *Trichoplusia, Dactyloplusia* and *Agrapha*, but a wider survey of species needs to be performed before the two (or more) forms here coded as state 1 can be adequately distinguished.

150 *Harpe a blunt, tubular process* **(0)**/*harpe a strongly dorsally and inwardly curving hook* (Fig. 369) **(1)**/*base of harpe also with an upcurving shorter hook forming a pincer-like structure* (Fig. 370) **(2)**. This hooked modification of the harpe curves towards the midline when the valves are closed, whereas that in character 149 curves in the plane of the valve towards the valve base.

151 *Valve apically entire* **(0)**/*valve apically deeply cleft, costa and sacculus separate* (Fig. 387) **(1)**.

152 *Valve much longer than wide* **(0)**/*valve ± as long as wide, overall outline somewhat trapezoid* (Fig. 375) **(1)**.

153 *When closed, valves lie in a lateral position, easily opened flat* (Fig. 389) **(0)**/*when closed valves lie ventrally or subventrally, difficult to open flat* (Fig. 388) **(1)**.

154 *Transtillae fused dorsally above aedeagus and produced posteriorly as a broad, blunt, triangular point* (Fig. 346) **(1)**/*transtillae separate or, if fused, not produced as a broad, blunt, triangular point* (Fig. 344) **(0)**. The euteliines lack transtillae and are coded * for this and the next character.

155 *Transtillae a single bar, though often curved, angled or broadly triangular* (Fig. 344) **(0)**/*transtillae laterally bifurcate into two thin bars diverging approximately at right angles; one passes dorsally over the aedeagus and fuses with its opposite number, the other runs lateral to the aedeagus* (Fig. 345) **(1)**. *Omorphina* has thin, fused bars passing over the aedeagus but no lateral bars. *Allagrapha* has broad, ill-defined lateral bars that may be homologous to the thin, heavily sclerotized, well-defined bars in *Sclerogenia* and *Erythroplusia*, but more species need to be investigated to confirm or refute this possibility.

Aedeagus

156 *Aedeagus large and thick* **(0)**/*aedeagus very thin and small, relative to the rest of the genitalia* **(1)**. This is a 'Gestalt' character, very difficult to define objectively but easy to recognize in the apomorphic state.

157 **Cuticular simplex arising dorso-basally on aedeagus, coecum ± absent* (Fig. 390) **(0)**/*cuticular simplex arising distinctly sub-basally, coecum distinct and of same diameter as aedeagus* (Fig. 391) **(1)**/*coecum distinct and bulbous* (Fig. 392) **(2)**. In some plusiines, the bulbous coecum is only just discernible as a slight increase in the diameter over the apical diameter (e.g. *Antoculeora*). In those genera exhibiting state 0 (e.g. *Oncocnemis*), the aedeagus in ventral view is of constant diameter (Fig. 393) and in lateral view, the ventral basal curvature is often more gradual than the dorsal basal curvature (Fig. 390) (e.g. *Cucullia*).

158 *Aedeagus generally sclerotized* (Fig. 393) **(0)**/*sclerotization apically restricted to a ventral band that gradually broadens onto the coecum* (Fig. 394) **(1)**/*sclerotization restricted to a thin ventral band along the entire length of the aedeagus distally, broadening somewhat abruptly onto the coecum* (Fig. 395) **(2)**. Also, the ventral band of state 2 is extremely well defined laterally, the edges being straight and parallel. The rest of the aedeagus is entirely membranous. In state 1, the ventral band merges somewhat into the membranous area laterally.

159 *Vesica ± covered for entire length in small, basally-directed spines* **(1)**/*vesica not so ornamented* **(1)**.

160 *When inverted, vesica very strongly and distinctly serpentine* (Fig. 406) **(1)**/*vesica not folded thus when inverted* **(0)**.

161 *Base of ductus ejaculatoris with a small, oval, sclerotized plate* **(1)**/*without* **(0)**.

162 *Vesica with an isolated, subapical cornutus (SAC)* **(1)**/*without* **(0)**. *Paectes* has two cornuti, one of which could be interpreted as subapical but, as the form of the vesica is short and inflated, rather than long and tubular, as in the plusiines, *Paectes* was coded 0. *Caloplusia* has a spinose, sclerotized plate in the approximate position of a SAC but was coded 0. *Autoplusia* bears a large, lateral cornutus about halfway along the vesica that could be interpreted as a SAC. This would, however, require that either the SAC has moved from a subapical to a median position on the vesica or that a large portion of the ductus ejaculatoris has become inflated and gained a large field of numerous small cornuti. It is more parsimonious to interpret *Autoplusia* as having no SAC. Similarly, *Palaeographa* has a recurved hook about halfway along the vesica that also is not homologous to a SAC. A SAC was reported and illustrated in *Eutheiaplusia* by Dufay (1970*a*) but was absent from the specimen examined in this study. The genus was coded 0. SACs were also occasionally absent in specimens of *Zonoplusia* and *Polychrysia*. In *Rachiplusia*, the SAC is double.

163 *SAC apically swollen* (Figs. 408, 409) **(1)**/*apically tapered* (Fig. 403) **(0)**. In *Adeva*, the SAC is short and therefore somewhat stubby. It is nevertheless not apically swollen. Taxa coded 0 for character 162 were coded * for characters 163–166.

164 *SAC arising from a circular, concave plate that has a somewhat irregular margin* (Figs. 362–365) **(1)**/*SAC arising from vesica without a differentiated, plate-like base* **(0)**.

165 *SAC arising apically from a lateral diverticulum* **(1)**/*SAC arising directly from the main vesica tube* **(0)**. The SAC of *Plusia* arises at the *base* of a diverticulum and was coded 0.

166 *SAC tubular* (Fig. 403) **(0)**/*SAC dorsally grooved* (Fig. 404) **(1)**/*edges of groove produced dorsally as 'wings'* (Fig. 405) **(2)**.

167 *Vesica with a membranous sac invaginated from the apex of the basal RHS vesica sclerotization and projecting anteriorly within the vesica* (Figs 397, 401) **(1)**/*vesica without such a sac* **(0)**. This sac is the 'bulbous lock' of Callahan (1960). In *Trichoplusia, Thysanoplusia, Argyrogramma* and *Stigmoplusia*, the sac is small and ± fused to the vesica sclerotization internally. In *Plusiotricha*, the sac is very long, reaching internally almost to the apex of the coecum.

168 *Base of vesica membranous and smooth* **(0)**/*internally granular, often forming a distinct annulus* **(1)**.

169 *Basal vesica sclerotization apically confluent with the membranous part of the vesica* (Fig. 397) **(0)**/*basal sclerotization produced ventrally as a blunt, apical point* (Figs 398, 399) **(1)**/*apical point elaborated into a large, blunt, recurved hook* (Fig. 407) **(2)**. The recurved hook in *Abrostola* is subventral on the LHS, rather than ventral but is interpreted as a further development of the ventral blunt point found in *Mouralia*.

170 *Vesica with a large, RHS, membranous diverticulum distal to the basal sclerotization bearing a field of cornuti on its outer-distal surface* **(1)**/*without such a diverticulum* **(0)**. In *Mouralia*, the field of cornuti is reduced to a small, sclerotized plate with several short cornuti.

171 *Vesica sub-basally with a dorsal, isolated patch of broad, curved, short, pointed cornuti* (Fig. 396) **(1)**/*without* **(0)**. In *Lamprotes*, the cornuti are connected to a LHS, lateral, sclerotized bar. Similar features are found in other genera (e.g. *Antoculeora, Sclerogenia*), but the location and apparent origin do not appear to be the same as for the cornuti here coded by state 1.

172 *Vesica with two short, straight, pointed cornuti dorsally distal to the apex of the basal sclerotization* (Figs 397, 401) **(1)**/*without* **(0)**.

173 *Basal sclerotization of vesica on RHS uniform* **(0)**/*modified and reduced to a lateral, longitudinal band,*

differentially sclerotized dorsally and ventrally (Fig. 400) **(1)**. Plesiomorphically, the base of the aedeagus appears to have been ± uniformly and heavily sclerotized, forming a basal, permanently everted annulus. In many plusiines, this basal sclerotization has been reduced to two lateral bars, one (commonly the LHS) or both of which are also frequently absent. In the Argyrogrammatini, the RHS bar represents the only basal sclerotization of the vesica and is inverted when the vesica is inverted and retracted. Further, this bar has heavier dorsal and ventral sclerotization, which gives it a grooved appearance, and in extreme instances (e.g. *Plusiopalpa*), the RHS bar appears to be longitudinally split. Some other species also have a RHS bar as the only basal sclerotization (e.g. *Rachiplusia*) but in these taxa, the bar is uniformly sclerotized. In *Zonoplusia*, the sclerotization is reduced to two, short, rudimentary bars, while the dorsal part is incomplete basally in *Eutheiaplusia*. The bar is very thin in *Stigmoplusia* but the differential sclerotization can be discerned in the somewhat spatulate apex.

174 *Basal RHS lateral sclerotization of vesica produced and turned dorsally to form a smooth, convex, rounded plate* (Figs 397, 401) **(1)**/*not* **(0)**.

175 *Sub-basal RHS auricular cornutus present* (Figs 383, 384, 385) **(1)**/*absent* **(0)**.

Female abdomen A1–7

176 *Pleural membrane of A7 thin, as on A2–6* **(0)**/*pleural membrane of A7 thickened, white, apparently glandular and often produced into a shallow pocket* **(1)**. The A7 pleural membrane in *Puriplusia* is only slightly thickened and apparently glandular. The thickening in *Allagrapha* is restricted to a shallow pouch on the posterior margin of A7. *Autoplusia* possesses a shallow pouch also, which is produced into a deep, conical invagination in *'Syngrapha' gammoides*. *Loboplusia* has a pleuron 7 that appears to be glandular but is not thickened. It is, however, difficult to be certain, so the genus was coded 0. In one of the two specimens of *Brachionycha*, pleuron 7 is thickened and white but is not apparently glandular. Nevertheless, the genus was coded 1.

177 *Lateral edges of T7 convex or ± straight* (Fig. 224) **(0)**/*concave* (Fig. 225) **(1)**. This character is almost certainly correlated with the last. The lateral margin of T7 in *Allagrapha* is only slightly concave (probably the result of the thickened area of pleuron 7 moving to the posterior margin of the segment), while in *Puriplusia*, the margin is straight (probably due to the pleuron in this genus being very slightly modified). The lateral margins of T7 in *Loboplusia* appear concave and the genus was scored 1, although the condition is somewhat uncertain. If the lateral margins are concave, and characters 176 and 177 are correlated, then it would be predicted that the examination of fresh specimens of *Loboplusia* would reveal, at least, a glandular, slightly thickened pleuron 7.

178 *Post-spiracular bar and anterior apodeme of segment St2 unmodified, pleural pouch absent* (Fig. 234) **(0)**/*post-spiracular bar and anterior apodeme of St2 modified to support a large pleural pouch* (Figs 230, 231, 233) **(1)**/*as (1) but pleural pouch small and partially concealed by the tympanal hood* (Fig. 232) **(2)**. This character was frequently unobservable in many specimens due to loss of the relevant parts on removal of the abdomen or during subsequent preparation. *Adeva, Polychrysia, Eosphoropteryx, Chrysanympha, Lophoplusia* and *Paectes* were scored, by necessity, from male specimens. *Chalcopasta* lacks a post-spiracular bar.

Anal papillae & A8–A9 + 10 intersegmental membrane

179 *Anal papillae ± square or tapered apically, inner and outer surfaces parallel in dorso-ventral plane* (Fig. 414) **(0)**/*anal papillae flared apically, inner surface partially or fully facing posteriorly* (Figs 417, 418) **(1)**.

180 *Inner surface of anal papillae membranous and devoid of setae (except for the extreme apex)* (Fig. 414) **(0)**/*inner surface densely setose* (Figs 417, 418) **(1)**.

181 *Apex of anal papillae entire* (Figs 414, 417) **(0)**/*apex with fine, irregular, setose prominences, giving a frayed appearance* (Fig. 418) **(1)**.

182 *Anal papillae setae long, fine and undifferentiated* (Fig. 420) **(0)**/*anal papillae with a dorso-ventral line of strong, pale-socketed setae, one-third to half way from the base, remaining setae mostly small and fine* (Figs 414, 415, 416) **(1)**. *Oncocnemis* has a central area with very stout, bluntly pointed setae sub-basally and a subapical row of similar but recurved setae. However, this setal type is autapomorphic for the genus and, because the basal and apical setae are of the long, fine type found in the other outgroup genera, *Oncocnemis* was coded 0.

183 *Anal papillae ± square, longer than wide or highly elongate* (Figs 414, 415, 416) **(0)**/*anal papillae short, distinctly wider than long* (Fig. 419) **(1)**. The plesiomorphic condition encompasses all anal papilla forms from the square, somewhat apically lobed type of most plusiines to the highly elongate, pointed type of *Brachionycha* and *Chalcopasta*. The form found in the euteliines and stictopterines

has been coded separately above (character 179) and the genera of these subfamilies are coded * for character 183.

184 *Membrane between A8 and anal papillae dorsally extended as a pouch* (Fig. 412) **(1)**/*membrane not so modified* (Fig. 413) **(0)**. The presence of the pouch has the effect, when everted and extended, of turning the anal papillae ventrally. In addition, the pouch may be strongly evaginated but this state proved too difficult to score consistently and was not employed.

185 *Base of posterior apophysis dorsally membranous or with a sclerotized flange indistinctly differentiated from the base of the anal papilla* (Figs 416, 420) **(0)**/*dorsal flange of posterior apophysis sub-basal, distinctly separated from the base of the anal papilla and often elongate and leaf-like* (Figs 414, 415) **(1)**. Many plusiines possess a basal flange on the posterior apophysis but only in the Argyrogrammatini is it distinct from the base of the anal papilla. In other genera (e.g. *Allagrapha, Puriplusia, Lophoplusia, Anagrapha*), the flange is an irregular sclerotized patch in the angle between the anal papilla and the apophysis or on the apophysis but connected to the base of the anal papilla by a semi-sclerotized zone of granular membrane.

186 *Membrane between lamina post-vaginalis (LPV) and anal papillae unmodified, extension of anal papillae ventrally easy* **(0)**/*membrane between LPV and anal papillae short, thickened and invaginated, preventing protraction of anal papillae ventrally* **(1)**.

A8, ostium bursae & antrum

187 *T8 uniformly sclerotized laterally* (Fig. 424) **(0)**/*T8 with a subdorsal, longitudinal, desclerotized band, the ventral edge of which is continuous with the dorsal edge of the anterior apophysis* (Figs 422, 423) **(1)**. *Chalcopasta* also has a desclerotized band but this has its apex along the midline of the anterior apophysis, so that the ventral edge of the desclerotization is ventral to, not continuous with, the dorsal edge of the anterior apophysis. In *Lophoptera* and the euteliines, the anterior apophysis is absent (see 190). All of these genera were coded 0.

188 *Anterior edge of T8 ventral to anterior apophysis flat* (Fig. 424) **(0)**/*invaginated as a dorso-ventral groove, with a ventral pocket* (Figs 421, 422, 423) **(1)**. The ventral pocket is very small in *Mouralia* but is enlarged, inflated and somewhat recurved in *Abrostola*.

189 *T8 irregularly cut back antero-subventrally below the origin of anterior apophysis, leaving the ventral base of anterior apophysis 'free'* (Fig. 425) **(1)**/*T8 not cut back antero-subventrally, base of anterior apophysis ventrally continuous with anterior edge of T8* **(0)**. State 1 for this character is variable in its expression. *Antoculeora* was coded 0 although its genitalia are so highly modified as to render the possible expression of state 1 very difficult.

190 *Anterior apophysis present* (Figs 422–425) **(0)**/*absent* (Figs 426, 429) **(1)**.

191 *Ventral margin of antrum not evaginated and projecting beyond the posterior edge of intersegmental membrane A7–A8* (Fig. 439) **(0)**/*ventral margin of antrum produced as an evaginated spinose or heavily sclerotized projection over the ostium bursae* (Figs 427, 428, 435) **(1)**. This probably corresponds to the 'classic' plusiine character of 'ostium bursae unprotected/protected'. Many, probably convergently derived, conditions are included under the apomorphic state. In *Allagrapha, Diachrysia* and *Brachionycha*, the evagination is poorly sclerotized and membranous. In contrast, in *Palaeographa* and *Caloplusia*, the evagination is very strongly sclerotized and the intersegmental membrane is fused to the projection ventrally. *Autoplusia* is coded 0 as *A. egena* exhibits the plesiomorphic state. However, *'Syngrapha' gammoides* has a very weakly developed apomorphic condition, similar to that found in *Antoculeora*. The state in *Loboplusia* is suspected to be 0 but it is difficult to say as most of the membrane anterior to the lip of the antrum has been removed in the preparation of the slide. In *Puriplusia* and *Macdunnoughia*, the evagination is limited to the subventral area.

192 *Lateral edges of antrum unmodified* **(0)**/*produced as two ± spinose pads lateral to the ostium bursae* (Fig. 431) **(1)**/*further fused with similar projections from the dorso-lateral corners of the antrum to form recurved, spinose grooves* (Fig. 432) **(2)**. Many of the genera with broad antra (196:1), especially among the outgroups, have somewhat similar lateral grooves to those found in *Puriplusia* and *Macdunnoughia* but are not heavily spinose or as deeply invaginated.

193 *Ventral margin of antrum and intersegmental membrane A7–A8 ventrally with short, dense, upright scales* (Fig. 433) **(1)**/*without* **(0)**. The entire female genitalia in *Diloba* are surrounded by a dense pad of upright, black scales. These, however, occur primarily on T7 and St7 and are considered non-homologous to the upright antrum-mouth scales found in *Allagrapha* and other genera.

194 **Antrum without setae* **(0)**/*antrum with 1–3 setae subventrally or laterally* (Fig. 435) **(1)**/*antrum with several setae along inner, ventral edge* (Fig. 434) **(2)**. *Brachionycha* has numerous setae lateral and subventral to the antrum but, as these are a continuation of the generally setose condition of T8 and

not a discrete patch, *Brachionycha* was coded 0. The setae along the inner, ventral edge of the antrum in *Diloba* also form a continuation of those found along the posterior margin of A8 but the genus was coded 2 because of their localized occurrence. However, it remains possible that the condition found in *Diloba* represents a convergent development from the condition found in *Brachionycha* rather than a homologue of that found in *Pseudeva* and *Plusidia*.

195 *Anterior edge of T8 ± level with ostium bursae* **(0)**/*T8 ventrally produced anteriorly to lie along the antrum dorsally and exceeding it* (Figs 426, 429) **(1)**. This extension of T8 antero-ventrally may represent a highly modified anterior apophysis (*cf.* character 190). This is suggested by the extension bearing an apical, dorsal small lobe. However, *Anuga* has a lateral anterior bump on the margin of T8 in the position often occupied by the anterior apophysis in other genera. Therefore, until the Stictopterinae and Euteliinae are examined in more detail, the present interpretation will be adhered to. In *Lophoptera*, the extensions are apically highly modified into a pair of spinose pads. See also character 202.

196 *Antrum a distinctly invaginated, often heavily sclerotized, structure* (Fig. 439) **(0)**/*antrum a broad, shallow, open bowl, ostium bursae somewhat exposed* (Fig. 434) **(1)**. *Brachionycha* and *Stictoptera* have narrow, shallow antra and were coded 0. *Diachrysia, Allagrapha, Puriplusia* and *Macdunnoughia* have invaginated but still somewhat open antra with marginal folds (see character 191) that protect the ostium bursae. These genera were coded 0.

197 *Antrum at least with sclerotized granulations, often very heavily sclerotized, well differentiated from ductus bursae* **(0)**/*antrum membranous, barely differentiated from the ductus bursae* **(1)**.

198 **Antrum sclerotization (if present) free from T8 or continuous only at the antero-ventral corner* (Fig. 434) **(0)**/*antrum with two subdorsal, apically broad and truncate bars, T8 ventral edges extended towards the midline* (Fig. 433) **(1)**/*extended T8 and antrum subdorsal bars fused, membranous area between the ventral edges of T8 very narrow* (Fig. 437) **(2)**/*ventral edges of T8 fused; T8, LPV and antrum forming a single, sclerotized area* (Fig. 428) **(3)**. *Mouralia* shows a state similar to state 2 but the T8 edges are not parallel and have not been extended (as indicated by the presence, in this genus of setae along the inner, ventral edge of T8). Setae are absent along the ventral edge of T8 in taxa showing states 1–3 (but, it should be noted, such setae are also absent in several genera showing state 0; e.g. *Omorphina, Diachrysia, Allagrapha, Syngrapha*). *Pseudoplusia* has extended edges to T8 but no subdorsal bars from the antrum. *Autoplusia* is coded 2 (the state shown by both *A. egena* and *A. olivacea*) but *'Syngrapha' gammoides* displays state 3.

199 *Anterior apophysis arising approximately halfway down T8 in lateral view* (Fig. 430) **(0)**/*anterior apophysis arising approximately level with the ventral edge of T8* (Fig. 440) **(1)**. Taxa lacking apodeme 8 (character state 190:1) were coded *.

200 *Antrum large, heavily sclerotized, smooth, open and curved somewhat to the RHS* (Figs 437, 439) **(1)**/*antrum relatively small, often poorly sclerotized, with longitudinal folds and ridges, not forming an open cavity* **(0)**. The antra of *Eosphoropteryx* and *Palaeographa* are curved to the LHS.

201 *Membrane lateral and anterior to ostium bursae thin and unmodified* **(0)**/*membrane thick, white, folded and tough* **(1)**. The thickened membrane in *Allagrapha* is the same membrane as that coded in character 176 and is thus most probably convergent on that condition found in, for example, *Palaeographa*. The membrane in *Euchalcia* is only slightly thickened.

202 *T8 dorsally with anterior edge ± level with or anterior to the antrum* **(0)**/*T8 represented by a thin band dorsally, anterior edge posterior to the antrum* (Fig. 426) **(1)**. T8 in *Adeva* (Fig. 430) is reduced to a thin band dorsally but this is formed by a strongly cut-back edge from an anteriorly positioned anterior apophysis. It is considered to be an independent derivation from state 0 rather than homologous to the condition found in the euteliines and *Lophoptera*.

Ductus bursae & corpus bursae

203 *Ductus bursae (DB) short (less than half the length of abdomen), usually broad* (Fig. 458) **(0)**/*DB long (over three-quarters the length of the abdomen) and narrow* (Fig. 446) **(1)**/*DB over 2× as long as abdomen and very narrow* (Fig. 447) **(2)**.

204 *Long axis of corpus bursae (CB) ± parallel with long axis of DB* (Fig. 449) **(0)**/*long axis of CB ± at right angles to long axis of DB* (Figs 446, 447, 448) **(1)**.

205 *Membrane of CB, at point of entry of DB, unmodified* **(0)**/*thickened, white and folded* **(1)**.

206 *Median section of DB tubular or merely flattened* (Fig. 446) **(0)**/*median section expanded somewhat laterally with dorsally recurved edges* (Fig. 441) **(1)**. *Dactyloplusia* has a laterally expanded median section of the DB but the edges are not recurved.

207 *DB with a lateral LHS short pouch with thick walls* **(1)**/*without* **(0)**.

208 *CB relatively inelastic, ± maximum size when dissected* **(0)**/*CB with very elastic walls, very small when first dissected but can be very easily stretched to several times its original size* **(1)**.

209 **Ductus seminalis arising from apex of CB* (Figs 450, 461, 462, 463) **(0)**/*from fundus* (Fig. 444) **(1)**/*from an accessory bursa produced from the DB* (Fig. 460) **(2)**. There is considerable difficulty in some taxa (e.g. *Mouralia, Diachrysia, Puriplusia*) in deciding which of two pouches is an enlarged apex and which is the CB proper. In *Puriplusia*, the orientation of the grooves near the origin of the DB (character 213) suggests that there may have been a 180 degree change in the orientation of the CB so that the apex is now directed anteriorly. However, this is not certain and pending further work, *Puriplusia* is coded 1. The same situation may pertain to *Loboplusia*. In *Sclerogenia*, the apex is interpreted to be recurved and totally fused with and open to the CB. *Erythroplusia* (Fig. 453) is also very problematical. A fundular origin of the ductus seminalis is inferred but it could be that the CB is extremely reduced and the apex very elongate to give the observed 'boomerang-shape', resulting in the ductus seminalis then being interpreted as arising from the apex and changing the coding for the genus to 0. The second species of *Erythroplusia, E. pyropia*, is very similar to *E. rutulifrons* and is of no use in resolving this problem. Those genera exhibiting state 1 for character 207 also present difficulties. The ductus seminalis is interpreted as arising from the apex in *Trichoplusia* and *Thysanoplusia*, and from the fundus in *Zonoplusia* and *Eutheiaplusia*, but this is by no means certain. *Plusiopalpa* is interpreted as having a small, recurved apex, bearing the ductus seminalis, with a secondary large apical pouch present dorsal and posterior to it. The ductus seminalis in *Pseudoplusia* is considered to arise from a long, anteriorly-recurved apex that is slightly fused to the CB basally (see character 214). *Chrysodeixis* is interpreted as having a fundular origin but examination of other species in this genus (*C. acuta*, [Dufay, 1970*a*]; *C. illuminata*, BM noctuid slide 11649) shows a similar condition to that found in *Pseudoplusia*, but in which the origin of the recurved apex has moved to a position about halfway along the CB. The extreme fundular origin of the ductus seminalis in *C. chalcites* may merely represent the ultimate expression of this transformation. The origin of the CB from the DB in *Stictoptera* is less well defined than in most species but the ductus seminalis still appears to arise from the apex of the CB, rather than a lateral origin on the DB. A similar interpretation was followed for *Magusa, Paectes* and *Anuga*, although the condition found in *Lophoptera* casts some doubt on this interpretation. More work is evidently needed in the stictopterine-euteliine complex.

210 **CB with weakly defined and irregular folds and lines, often smooth* (Fig. 463) **(0)**/*with regular, elongate, longitudinal ridges, originating from dorsal and lateral longitudinal 'focal' ridges, which may or may not be sclerotized* (Fig. 464) **(1)**/*ridges forming a ± circular pattern* (Fig. 457) **(2)**.

211 *CB without a localized signum* **(0)**/*CB with a small, slightly concave, circular signum* (Fig. 457) **(1)**/*signum invaginated as a narrow internal ridge* (Fig. 465) **(2)**.

212 *CB with uniform internal ornamentation or, if several forms present, then these gradually merge one into another* **(0)**/*CB with a distinct discontinuity halfway along its length, separating a pale, membranous posterior half from an anterior half covered in sclerotized granulations and finer folding* (Figs 454, 456) **(1)**.

213 **Area of entry of DB into CB with large, strong, well sclerotized internal folds that extend onto the apex or rarely onto the fundus* (Figs 450, 451, 454, 455, 456) **(3)**/*ridges present and sclerotized but not strongly developed* (Figs 445, 449) **(2)**/*ridges not sclerotized, merely granular* (Fig. 452) **(1)**/*ridges absent* (Fig. 461) **(0)**. *Calophasia* has a smooth area of sclerotization in the dorsal angle between the DB and the apex, that may have a few folds. However, these folds are not extensive and the genus was coded 0. *Paectes* has a long series of diagonal, heavily sclerotized folds on the posterior section of the CB but these are not connected with folds arising on the DB and are not considered homologous to the folds found in *Autoplusia* and related genera. The apex and folds are highly reduced in *Allagrapha*, while in *Puriplusia*, they continue onto the fundus rather than the apex (but see 209).

214 *Apex recurved in dorso-ventral plane and somewhat fused basally to the CB* (Figs 443, 444) **(1)**/*apex not so modified* **(0)**.

215 *CB without a dorso-lateral RHS patch of thickened white membrane somewhat anterior of the entry-point of the DB* **(0)**/*such a patch present* (Figs 461, 462) **(1)**/*patch expanded into a shallow pouch* (Fig. 463) **(2)**/*expanded further into a large pouch or a long appendix in which the thickened membrane is present only apically* (Fig. 458) **(3)**.

Miscellaneous

216 *Colour pattern monomorphic* **(0)**/*pattern sexually dimorphic, males greyish, females brown* (Figs 82, 83) **(1)**. In *Autoplusia*, only *'Syngrapha' gammoides* is obviously sexually dimorphic in this manner. The difference is only barely discernible in other species of the genus (*A. egena, A. olivacea*). In

Sclerogenia, the females appear to be slightly duller than the males but this is not great enough to warrant the description 'sexually dimorphic'. *Cucullia* is also sexually dimorphic but shows a different type of variation (males have white hindwings, females brown) and was coded 0. *Stictoptera* is highly polymorphic but the various forms are not sex limited.

Analytical procedure

The data were analysed using David Swofford's program for inferring phylogenies using the principle of maximum parsimony, PAUP (version 2.2), run on the IBM System/370 3032 at the Rutherford Appleton Laboratory. Due to the large size of the data set (57 taxa by 216 characters), the analysis was broken down into several subprocedures that were run separately at different times.

Initially, a simple Wagner tree was constructed using the addition sequence CLOSEST and setting HOLD (the number of trees held in memory at any one step of tree construction) equal to one. No branch-swapping was employed at this point. The result was a single cladogram of 659 steps and a consistency index (Kluge & Farris, 1969) of 0·466.

This cladogram was subsequently used as an input to a branch-swapping analysis (using the option SWAP = ALT in an attempt to reduce the run time), which also invoked the MULPARS option to check for the existence of multiple, equally-parsimonious cladograms. A default maximum of 50 cladograms was found, with the reduced length of 648 steps and a consistency index of 0·474.

These 50 cladograms were then evaluated in order to determine the topological differences between them. It was found that they consisted of five pairs, one triplet and one quadruplet of mutually-exclusive subcladograms and a single alternative that was mutually exclusive to all but one of the five pairs. Combining these alternative subcladograms gives a minimum number of 448 equally-parsimonious cladograms for this data set.

In order to determine which of these 448 possibilities represented the best hypothesis of the interrelationships of the plusiine genera, the apomorphy lists for six (output cladogram numbers 27, 29, 39, 44, 45 and 46) were obtained, which covered all the alternative subtopologies. A single preferred cladogram was then identified by a process of character analysis and evaluation, which is described in the next section.

A second analysis was then performed on a restricted data set, with the outgroup taxa (*Chalcopasta-Anuga*, 48–58) excluded. The intention was to check whether the 64 alternative topologies found for the plusiines alone were exhaustive or whether, by restricting MAXTREE (the maximum number of equally-parsimonious trees held in memory during a branch-swapping procedure) to 50, any had been missed. To save computing time, the preferred topology (see below) was entered as the initial user-tree and branch-swapping performed using SWAP = ALT, MULPARS and MAXTREE = 50. The initial cladogram of 451 steps (it is worth noting in passing that 197 or 30·6% of the steps on the original cladogram occurred outside the Plusiinae) was, surprisingly, reduced in length by two steps to 449 (consistency index not calculated) and only 16 alternatives were found. The two missing pairs were those involving the location of *Loboplusia* and the sequence of branching among the various tribes and subtribes (see below).

Initially, it was suspected that this additional shortening of the cladogram was an artefact caused by the omission of the outgroup taxa. Thus, a final analysis was undertaken in which one of the previously obtained outgroup topologies was added to one of the 16 plusiine topologies and the resultant cladogram entered as a user-tree.

Fitting of the data to this cladogram resulted in a length of 647, a reduction of one step. Thus the 50(+) cladograms of 648 steps obtained originally did not represent the minimum-length as was first thought. The branch-swapping algorithm applied in the first analysis had failed to find the minimum-length topology before the MAXTREE limit of 50 had been reached. Further, it is unlikely that it would have been found even had MAXTREE been set to the system maximum of 150, given a minimum of 448 possible cladograms of 648 steps and the basal position of the swap necessary to locate the shorter cladograms of 647 steps. (The algorithm appears to perform its branch-swapping starting with pairs of terminal taxa and proceeding towards the base of the cladogram. Also, to find the 647-step cladograms, a swap involving the rearrangement of subcladograms of 8 or more taxa was required, based upon an initial topology that occurred only five times out of the original 50 cladograms and which was first found at cladogram 33.) Had the second analysis of the restricted data set not been performed, the existence of the 16 cladograms of 647 steps would never have been revealed.

However, examination and evaluation of the apomorphy lists of the 647-step cladograms demonstrated that the branching sequence of the major plusiine lineages was determined by very similar character state changes to those present on one subset of the rejected 648-step topologies. Thus, the minimum-length cladograms were rejected in favour of the 648-step, preferred cladogram referred to above. The full reasoning behind this decision is given below.

The 648-step cladograms

1. *Agrapha* and *Plusiopalpa*

Two subcladograms were found in which the positions of *Agrapha* and *Plusiopalpa* differed. Subcladogram 1 (Fig. 9) places *Agrapha* as the sister-group of *Argyrogramma* + *Stigmoplusia* (*A*+*S*), and *Plusiopalpa* as the sister-group of *Acanthoplusia* + *Ctenoplusia* (*A*+*C*). Subcladogram 2 (Fig. 8), in contrast, treats *Plusiopalpa* as the sister-group of *A*+*S*, and *Agrapha* as the sister-group of these three genera plus *A*+*C*. The different topologies are due to alternative interpretations of 13 characters (61, 79, 83, 86, 87, 88, 92, 98, 105, 130, 138, 144, 162). An evaluation of these characters is required in order to decide which subcladogram represents the best cladistic hypothesis of the relationships between the six genera.

61: The sequence of suppression of the male fore-tibial spines forms a clear, non-homoplasious transformation series on subcladogram 2, where state 1 characterizes *A*+*S* + *Plusiopalpa*, state 2 unites *A*+*S*, and state 3 is autapomorphic for *Argyrogramma*. Character 61 is not as convincing on subcladogram 1, on which states 1 and 2 are interpreted as independent derivations from state 0. On both cladograms, state 1 is also convergently derived in *Plusiotricha* and in the stictopterines (see also below). Thus character 61 supports subcladogram 2.

79: This character is problematical on both subcladograms. The expected transformation series, in which the hair tufts on segments A5 and A6 both gain discrete edges (state 1), followed by independent losses of such margins on A6 (state 2) and A5 (state 3), did not appear. On subcladogram 1, *A*+*S* + *Agrapha* are characterized by the change 0 → 3 (discrete edges on A6 only), followed by independent derivations of state 2 in *Stigmoplusia* (A6 only → A5 only) and state 1 in *Agrapha* (A6 only → A5 and A6). On subcladogram 2, state 1 in *Agrapha* is independently derived from state 0, with *A*+*S* characterized by the change 0 → 3 followed by the autapomorphic change 3 → 2 in *Stigmoplusia*. Alternative optimizations on subcladogram 2 are equally ambiguous. One assigns state 0 to the node immediately ancestral to *Argyrogramma* and *Stigmoplusia*, in which case states 2 and 3 respectively are independently derived in the two genera from state 0. Alternatively, the internal node could be assigned state 2, whence *Argyrogramma* is characterized by the autapomorphic change 2 → 3. Subcladogram 1 is marginally favoured in that character 79 delimits a monophyletic group on this subcladogram but the transformation series is not very satisfactory, despite a character consistency of 1·000 (true also of subcladogram 2).

83: This character is one of the most highly homoplasious in the data (consistency = 0·313). However, state 4 is only found in *Plusiopalpa* and *Argyrogramma* and thus lends weak support to subcladogram 2 (*Stigmoplusia* possess the widely distributed state 3).

86: Subventral accessory pockets unite *A*+*S* and *Agrapha* as a monophyletic unit and thus support subcladogram 1. On subcladogram 2, these pockets have to be hypothesised to have developed independently in the two groups (as well as in *Acanthoplusia*, which is also true on subcladogram 1).

87: Although optimization of this character on subcladogram 2 suggests an initial gain followed by a 'monophyletic' loss in *A*+*S* + *Plusiopalpa*, an equally parsimonious interpretation is one of independent gain in *A*+*C* and *Agrapha*. This is also the optimized distribution of states for this character on subcladogram 1 and thus character 87 is of no use in deciding which subcladogram should be accepted.

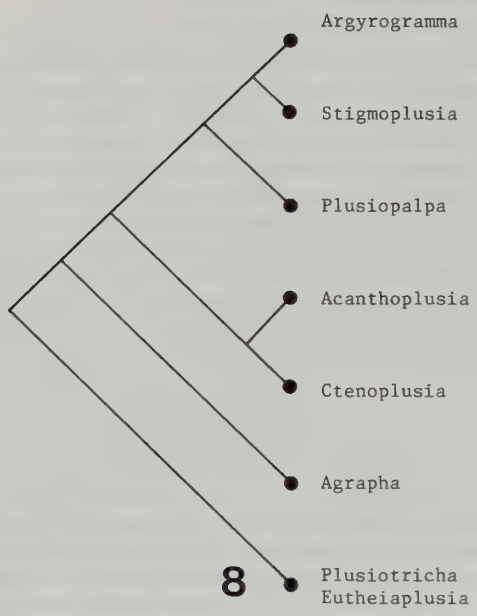
88, *98*, *105*: These characters show similar distributions to the last, in that they can be interpreted on subcladogram 1 as having been independently gained (*Agrapha* and *Argyrogramma*) or gained once (thus characterizing *A*+*S* + *Agrapha*) with subsequent reversal (in *Stigmoplusia*). The former distribution is that found on subcladogram 2 and so characters 88, 98 and 105 are also irrelevant to the decision.

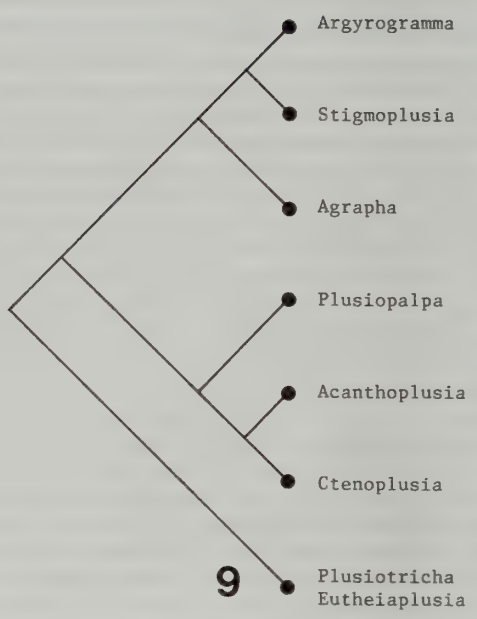
92: On subcladogram 1, the state changes 1 → 3 and 1 → 2 arise independently and characterize *A*+*S* and *A*+*C* + *Plusiopalpa* respectively. On subcladogram 2, state 3 transforms into state 2, resulting in the exclusion of *Agrapha*. Although both subcladograms are equally supported, other shared similarities of the secondary hair pencil attachments between *A*+*S* and *Plusiopalpa* (see below) tip the balance slightly in favour of subcladogram 2 and its sequential transformation series.

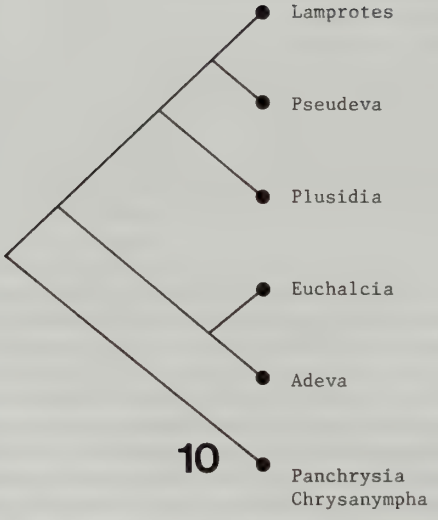
130: A juxta that is free from the saccular flanges also occurs in *Pseudoplusia* + *Chrysodeixis* and thus offers only weak support for the monophyly of *A*+*S* + *Agrapha* (subcladogram 1).

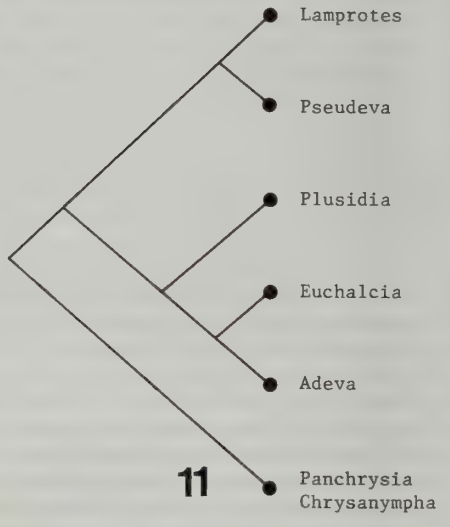
138: Similarly, but conversely, the monophyly of *A*+*S* + *Plusiopalpa* (subcladogram 2) can be weakly supported by the monophyletic reversal of this character.

144: This character (the degree of development of the clavus) shows an extremely high amount of homoplasy (character consistency index = 0·133) and thus is very suspect. Both subcladograms postulate the reduced condition (state 1) to be plesiomorphic for the six genera. Subcladogram 1 hypothesises independent reversals to a long clavus (state 0) in *Argyrogramma* and *A*+*C* +









Figs 8–11 8, subcladogram 2, depicting *Plusiopalpa* as the sister-group of *Argyrogramma* + *Stigmoplusia* and a relatively basal position for *Agrapha*. 9, subcladogram 1, illustrating the alternative placements of *Plusiopalpa* and *Agrapha*. 10, subcladogram 3, showing *Plusidia* as the sister-group of *Lamprotes* + *Pseudeva*. 11, subcladogram 4, the alternative position of *Plusidia* as the sister-group of *Euchalcia* + *Adeva*.

Plusiopalpa, while subcladogram 2 suggests a reversal above the point where *Agrapha* branches off, followed by a re-reversal to state 1 in *Stigmoplusia*. Both subcladograms include an autapomorphic extreme reduction in *Agrapha*. Given the number of steps associated with this character, it is considered to be too unreliable and of little use, especially with regard to the current decision.

162: *A+S + Agrapha* are united on subcladogram 1 by the (highly homoplasious) gain of a subapical cornutus (SAC). However, examination of species other than the type species shows a SAC to be general in *Ctenoplusia* (Dufay, 1970*a*). *C. limbirena* is apparently aberrant in lacking one, so further increasing the homoplasy in this character. Thus, absence of a SAC is rejected as demonstrating relationship.

Overall, the decision between the two topologies was close. Subcladogram 1 is supported by character 86 and weakly by characters 79 and 130. Subcladogram 2 is supported by character 61 and weakly by characters 83, 92 and 138. On balance, the evidence in favour of subcladogram 2 appears slightly better and it is accepted over subcladogram 1. However, the most expedient solution may be the consensus tetrachotomy (see below).

2. *Plusidia*

Two subcladograms were found in which the position of *Plusidia* was ambiguous. In subcladogram 3 (Fig. 10), *Plusidia* is treated as the sister-group of *Lamprotes + Pseudeva* (*L+P*), while in subcladogram 4 (Fig. 11), the genus is placed as the sister-group of *Euchalcia + Adeva* (*E+A*). Ten characters (6, 41, 42, 58, 144, 154, 171, 186, 194, 205) are involved in the ambiguity.

Five characters support a sister-group relationship between *Plusidia* and *E+A*. Of these, four are reversals in highly homoplasious characters (6, 41, 42, 58), while the apomorphic state for the fifth (205) also characterizes *Cucullia, Trichoplusia* and *Plusiotricha + Eutheiaplusia*. The evidence is thus not very strong. In contrast, the five characters that suggest that *Plusidia* is most closely related to *L+P* include two (171 and 186) that are unique and unreversed. Further, the transformation series of character 194 is only homoplasious insofar as state 1 is independently derived in the outgroup taxon *Diloba*, and there is doubt as to the homology of this condition and that found in *Plusidia + L+P* (see below). Character 154 is found in its apomorphic state in *Panchrysia, Chrysanympha* and *E+A* and thus is interpreted as reversed in *Plusidia + L+P* on subcladogram 3, while the last, character 144, is one of those for which extreme doubt was expressed in the previous section regarding reliability.

Overall, there can be little doubt, after evaluating the characters supporting the alternative subcladograms, that subcladogram 3 is to be preferred and *Plusidia* interpreted as the sister-group of *Lamprotes + Pseudeva*.

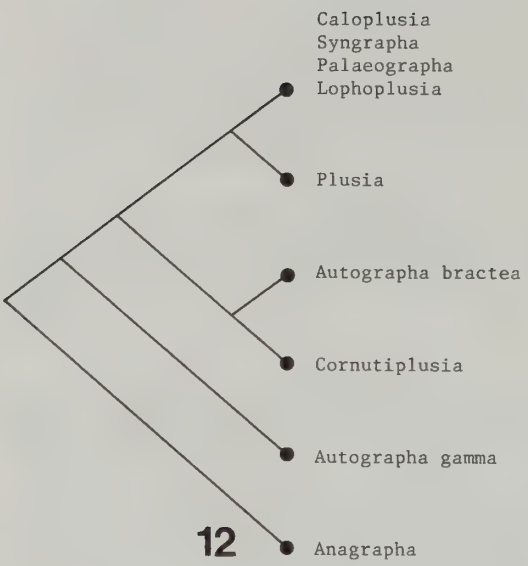
3. *Autographa, Cornutiplusia* and *Plusia*

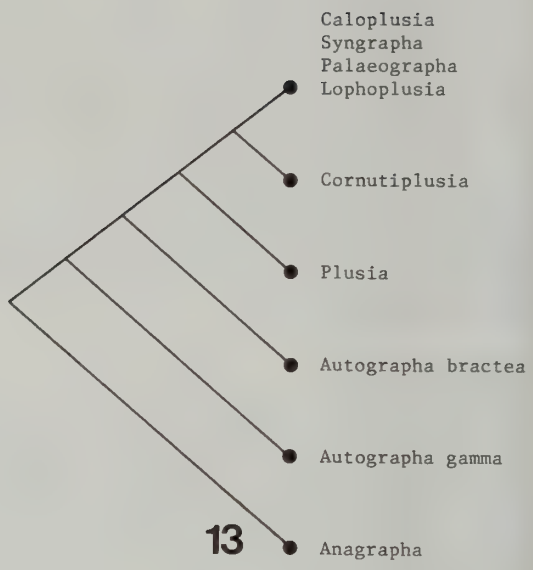
It was noted during the data collection that few synapomorphies were being found for *Autographa, Cornutiplusia, Plusia* and their immediate relatives. Thus, it was not unexpected when multiple, equally-parsimonious subcladograms were found that included these genera. In all of these subcladograms, there was a constant terminal cluster of four genera (*Caloplusia, Syngrapha, Palaeographa, Lophoplusia*; = *CSPL*) and a constant outgroup, *Anagrapha*. Between these taxa, four topologies were found that rearranged *Plusia, Cornutiplusia, Autographa gamma* and *A. bractea*.

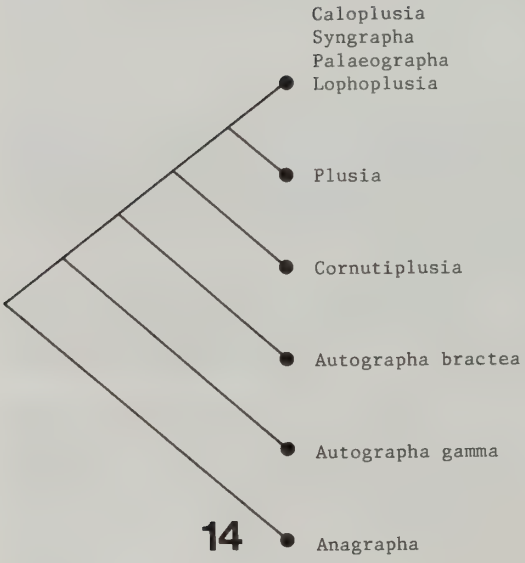
Three subcladograms, 5, 6 and 7 (Figs 12–14 respectively) agree in placing *A. gamma* as the basal taxon, while subcladogram 8 (Fig. 15) so places *A. bractea*. Three subcladograms, 5, 7 and 8, also agree in placing *Plusia* as the sister-group of *CSPL*, while subcladogram 6 places *Cornutiplusia* in this position. Subcladogram 5 differs from subcladogram 7 in placing *Cornutiplusia* and *A. bractea* as sister taxa. Four characters only are involved in differentiating the alternative topologies: 12, 64, 166 and 215.

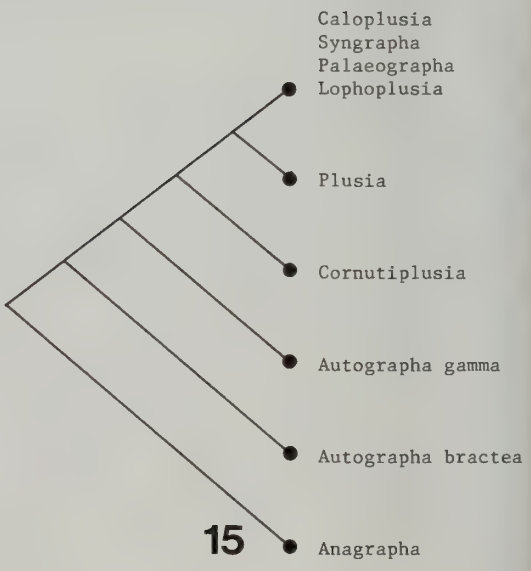
Character 12 is highly homoplasious (consistency index = 0·100). The apomorphic state varies from a mere silver spot between the reniform stigma and the cubital vein (as seen in *Antoculeora* and *Plusiopalpa*) to that in which the reniform stigma is almost entirely outlined in silver (a condition unique to *Lophoplusia* and perhaps not too far removed from the completely silver stigmata of *Plusia* and *A. bractea*). However, character 12 is one of the two characters that support a sister-group relationship on subcladogram 6 between *Cornutiplusia* and *CSPL*. The other character on this branch, character 64, is the 'classic' plusiine character of spined hind tibiae. This is also highly homoplasious; state 1 is also found in *Autoplusia* and state 2 in *Rachiplusia* and *Anagrapha*. The topology of subcladogram 6 is also supported by the observation that occasional spines occur in *Plusia* and *Autographa* (McDunnough, 1944).

Plusia is placed as the sister-group to *CSPL* on subcladograms 5, 7 and 8 by a synapomorphy in character 166. State 2, the distinctly winged subapical cornutus, was scored as autapomorphic for *Lophoplusia* and as 'not comparable' for *Palaeographa, Syngrapha* and *Caloplusia*, because the type species of these taxa lack subapical cornuti. That these three taxa are predicted to show state 2 is interesting. Several species of









Figs 12–15 The four alternative subtopologies involving *Autographa, Plusia* and *Cornutiplusia*. 12, subcladogram 5. 13, subcladogram 6. 14, subcladogram 7. 15, subcladogram 8.

Syngrapha, particularly those considered by Eichlin & Cunningham (1978) to be primitive (e.g. *S. ottolenguii* (Dyar), *S. viridisigma* (Grote), *S. orophila* (Hampson)), do bear subapical cornuti on the vesica and in one species, *S. epigaea* (Grote), the cornutus even appears to be winged (Eichlin & Cunningham, 1978: fig. 58a). Thus, the interpretation of *Plusia* as the sister-group of *CSPL*, on the basis of character state 166:1, may prove well-founded and is provisionally accepted here as the best cladistic hypothesis. Subcladogram 6 is thus rejected, despite the evidence furnished by character 64.

A. gamma is placed as the most basal taxon on subcladograms 5–7 because it displays the plesiomorphic state for character 215. The first apomorphic state is the presence of a dorso-lateral patch of thickened membrane on the corpus bursae and is found in *Plusia* and *Lophoplusia*. This is further elaborated into a shallow pouch (state 2) in *A. bractea* and into a large pouch or appendix (state 3) in *Cornutiplusia*. All subcladograms require a reversal from state 1 to state 0 in *Palaeographa* + *Syngrapha* + *Caloplusia*. Subcladogram 7 has what appears to be the worst optimization of states, requiring the derivation of state 2 directly from state 0, then a further autapomorphic development of state 3 in *Cornutiplusia*, together with a reduction in the structure, stage 2 → 1, along the branch leading to *Plusia* + *CSPL*. Subcladogram 8 is somewhat better in that independent derivations of states 2 and 3 from state 0 are postulated, a distribution of states also found on the rejected subcladogram 6. Subcladogram 5, however, unites *A. bractea* and *Cornutiplusia* using state 2 and then derives state 3 autapomorphically in the latter taxon. This interpretation is further supported by the observation that state 2 appears to be present in all the putative North American relatives of *A. bractea* except one, as judged from the figures and phylogenetic tree given by Eichlin & Cunningham (1978) (but see Clade analysis). Thus, the branching sequence, and associated character state changes, of subcladogram 5 is accepted as the best cladistic hypothesis of relationships for these genera.

4. *Loboplusia*

The genus *Loboplusia*, with its large amount of missing data and relatively simple male genitalia, was expected to be ambiguous in position. Two subcladograms were found; subcladogram 9 (Fig. 16) places *Loboplusia* as the sister-group of *Erythroplusia*, while subcladogram 10 (Fig. 17) hypothesises a sister-group relationship between *Loboplusia* and *Autoplusia* + *Antoculeora* + *Sclerogenia* (*AAS*). Eleven characters (6, 12, 59, 113, 142, 148, 155, 176, 177, 209) are involved in these alternative interpretations of the position of *Loboplusia*.

Loboplusia is grouped with *Erythroplusia* on the basis of three character state changes. The loss of the scale tooth on the forewing tornus (6) is highly homoplasious and of little importance. Similarly, the fundular origin of the ductus seminalis on the corpus bursae (209) appears to have been multiply derived, supporting the reservations outlined above regarding the correct interpretation of corpus bursae morphology. Finally, character 155 was scored as 'missing data' for *Loboplusia*, because the transtillae were torn. Thus, the presence of the apomorphic state of character 155 in *Loboplusia* is a prediction of the optimization procedure and not an empirical observation. The evidence supporting subcladogram 9 is therefore tenuous.

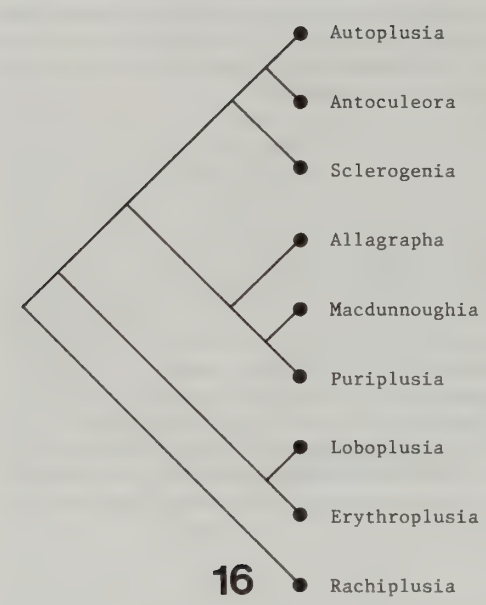
On subcladogram 10, *Loboplusia* is placed by four characters in a larger clade including *AAS* and a clade consisting of *Allagrapha, Macdunnoughia* and *Puriplusia* (*AMP*). Two of these characters, 142 and 176, are subsequently reversed on the branch subtending *Loboplusia*. The condition of character 177 was considered somewhat uncertain but does provide weak support for this topology. The apomorphic state of character 113 is shared by *Loboplusia* and *AMP*, and is considered to have reversed in *AAS*. Further, *Loboplusia* is placed as the sister-group of *AAS* by three characters, all with low consistency indices. Two (59 and 148) are reversals that occur several times elsewhere on the cladogram, while the third (12) was rejected above as unreliable.

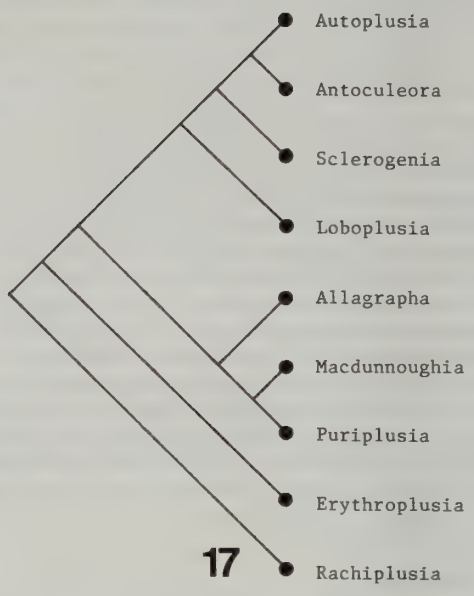
Overall, the evidence supporting each placement of *Loboplusia* is very weak, with subcladogram 10 being marginally preferable. However, until such time as further studies are performed and additional specimens become available, the best course may be to treat *Loboplusia* as forming a trichotomy with *Erythroplusia* and *AAS* + *AMP* (see below).

5. *Rachiplusia* and the branching sequence of the tribes and subtribes

The final pair of alternative topologies within the Plusiinae affects the fundamental branching pattern of the Argyrogrammatini and the three subtribes of the Plusiini: the Plusiina, Euchalciina and Autoplusiina. (The Autoplusiina are temporarily defined as *Rachiplusia, Erythroplusia, Loboplusia, AAS* and *AMP*.) In addition, there is ambiguity concerning the relationships of *Rachiplusia*.

Subcladogram 11 (Fig. 18) agrees well with the trees put forward previously by Ichinosé (1962*b*) (Fig. 2) and Eichlin & Cunningham (1978) (Fig. 3). Both the Argyrogrammatini and Plusiini, as currently recognized, are monophyletic. Within the latter, the subtribe Euchalciina is the sister-group of the Plusiina





Figs 16–19 16, subcladogram 9, showing *Loboplusia* as the sister-group of *Erythroplusia*. 17, subcladogram 10, with *Loboplusia* as the sister-group of *Sclerogenia* + *Antoculeora* + *Autoplusia*. 18, subcladogram 11, the topology of the tribal and subtribal branching that places *Rachiplusia* as the sister-group of the remaining Autoplusiina. 19, subcladogram 12, the alternative subtribal topology illustrating a paraphyletic Plusiini and with *Rachiplusia* as the sister-group of the Argyrogrammatini.

+ Autoplusiina. The genus *Rachiplusia* is placed as the most basal branch within the last of these subtribes.

The monophyly of the Plusiini is based upon three characters. Two of these (121 and 127) are moderately homoplasious but the last, character 117, is uniquely derived but reversed in *Antoculeora*. In this genus, the broad lateral flange of the pleurite is absent, a condition probably correlated with the autapomorphic form of the pleurite coded by character state 118:2. The sister-group relationship between the Plusiina and the Autoplusiina is based upon a single character, 116, the autapomorphic state of which is lost in *Antoculeora* (cf. character 117) and independently derived in *Anadevidia*. *Rachiplusia* is placed as the sister-group of the rest of the Autoplusiina based on reversals in three highly homoplasious characters (18, 59 and 148) and a change from state 0 to state 2 in character 213. Although this character is homoplasious (particularly when the outgroups are taken into consideration), further work may justify it and the position of *Rachiplusia* it supports.

The alternative subcladogram 12 (Fig. 19) is in considerable disagreement, in that the Plusiini is paraphyletic, not only with respect to the subtribal arrangement, but also because *Rachiplusia* is treated as the sister-group of the Argyrogrammatini. However, the supporting characters are very weak. The Argyrogrammatini, Autoplusiina and Plusiina are grouped together to the exclusion of the Euchalciina by two characters. The first, 116, was synapomorphic for the Autoplusiina and Plusiina on subcladogram 11, on which the presence of state 1 in *Anadevidia* (the basalmost member of the Argyrogrammatini) was interpreted as convergent. On subcladogram 12, state 1 is interpreted as uniquely derived but reversed in the Argyrogrammatini above *Anadevidia*. The second character state change is 83:0 → 3 and concerns the degree of development of the sternal hair pencils in the males. The sequence of state changes for character 83 is very complex and highly homoplasious. Very little confidence can be placed in it. The Autoplusiina and Argyrogrammatini are united by two reversals in characters 18 and 148, both of which are subject to multiple convergent gains and reversals. Finally, two character state changes support the sister-group relationship between the Argyrogrammatini and *Rachiplusia*: 14:0 → 2 and 110. The latter (whether the vinculum is V-shaped or Y-shaped) is trivial, homoplasious and can be discounted. 14 can also be rejected once its full transformation on subcladogram 12 is analysed. The complete series consists of 0 → 2 (*Rachiplusia* + Argyrogrammatini), 2 → 1 (*Anadevidia* only) and two convergent 0 → 2 changes (*Autoplusia, Mouralia*). The first two of these imply that seta 1 of the female frenulum was first lost and then partially regained as a rudiment in *Anadevidia*. The more parsimonious sequence morphologically, in which the seta is reduced and then lost, is precluded by the position of *Rachiplusia*. However, both interpretations for the origin of state 1 in *Anadevidia* (reduction as an intermediate step or as a terminal reversal) are allowed on subcladogram 11. Thus, on the basis of this, and on the evidence provided by characters 116, 117 and 213, subcladogram 12 is rejected and subcladogram 11 accepted as the best cladistic hypothesis for this section of the plusiine cladogram.

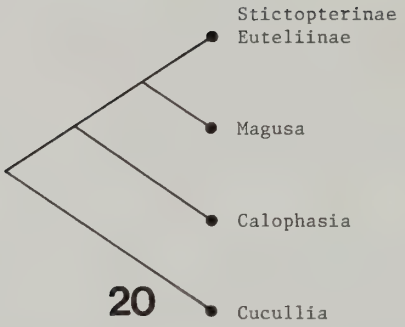
6. Outgroups

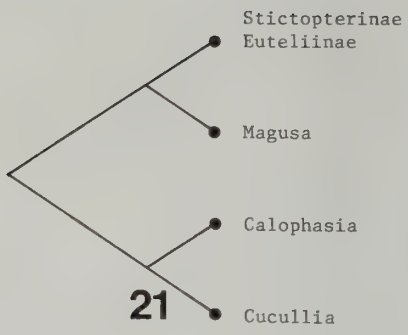
Due to the variety and 'taxonomic distance' between the outgroups (11 genera from four subfamilies), it was not surprising to find that there were many alternative topologies for them. Three constant features were found:

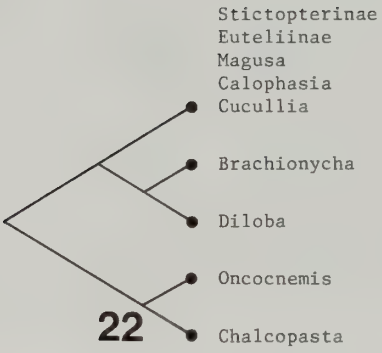
(a) *Oncocnemis* and *Chalcopasta* are sister-groups;
(b) *Brachionycha* and *Diloba* are sister-groups; and
(c) the Stictopterinae and Euteliinae are each monophyletic and together form a monophyletic group to which *Magusa* is the outgroup (= *SEM*).

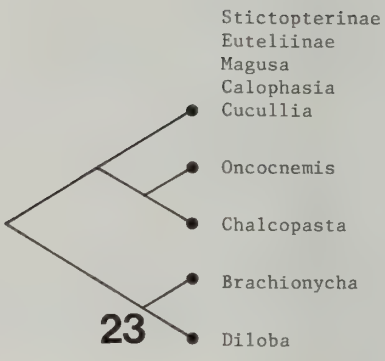
However, the sequence in which these three groups and the other two genera, *Cucullia* and *Calophasia*, clustered proved very variable. One pair of alternative topologies was found in which *Calophasia* + *Cucullia* + *SEM* formed a clade. The first (Fig. 20) places *Calophasia* as the sister-group of *SEM*; the second (Fig. 21) places it as the sister-group of *Cucullia*. Accepting this as a terminal taxon, three further topologies were found in which its sister-group was *Brachionycha* + *Diloba* (Fig. 22), *Oncocnemis* + *Chalcopasta* (Fig. 23), or these four genera together (Fig. 24). In addition, a non-exclusive alternative topology was found (Fig. 25) in which *Calophasia* + *Cucullia* was the sister-group of *Oncocnemis* + *Chalcopasta*, and *SEM* was the most basal clade. All these relationships have to be qualified by the statement that there is no guarantee that the root of the entire cladogram lies between the Plusiinae and the outgroups.

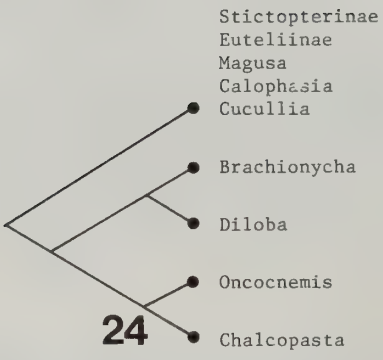
The precise resolution of the relationships of the outgroups is of secondary importance in this study. Thus, the decision as to which of the above alternatives is to be preferred is not critical. The topology that is depicted on the final preferred cladogram (see below) is that which places the Plusiinae nearest to the Stictopterinae, their erstwhile closest relatives, in order to evaluate the characters that support this relationship.

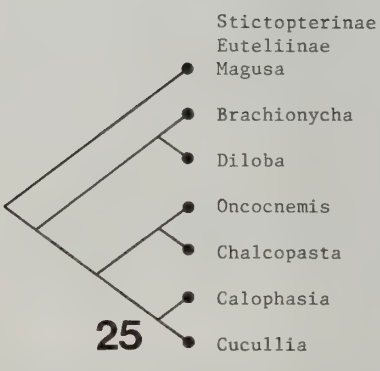












Figs 20–25 The alternative outgroup subtopologies. 20, outgroup subtopology 1. 21, subtopology 2. 22, subtopology 3. 23, subtopology 4. 24, subtopology 5. 25, subtopology 6. Note that subtopology 6 is an exclusive alternative to subtopologies 1–5.

The 647-step cladograms

Following removal of the outgroups, further global branch-swapping with the multiple parsimony option discovered a set of 16 cladograms. After reinstatement of the outgroups, these cladograms were found to be 647 steps long, one step shorter than those found in the earlier analyses that were described above. The 647-step cladograms are of similar topology to the rejected 648-step subcladogram 12, in that *Rachiplusia* forms the sister-group of the Argyrogrammatini, but differ in the branching sequence of the subtribes of the Plusiini (Fig. 26). Whereas, on subcladogram 12 of the 648-step cladograms, the Autoplusiina (less *Rachiplusia*) form the sister-group of the Argyrogrammatini + *Rachiplusia*, on the 647-step cladograms, it is the Plusiina that occupy this position. The 16 alternatives arise from the mutually exclusive topologies referred to previously as subcladograms 1/2 (*Agrapha*/*Plusiopalpa*), 3/4 (*Plusidia*) and 5/6/7/8 (*Autographa*/*Cornutiplusia*/*Plusia*). The presence of further alternatives in the outgroup taxa was not observed but all of the topologies found previously would be expected. Reversing the order of branching of the Plusiina and Autoplusiina (less *Rachiplusia*) appears to preclude the alternative topology that places *Loboplusia* as the sister-group to *Erythroplusia*.

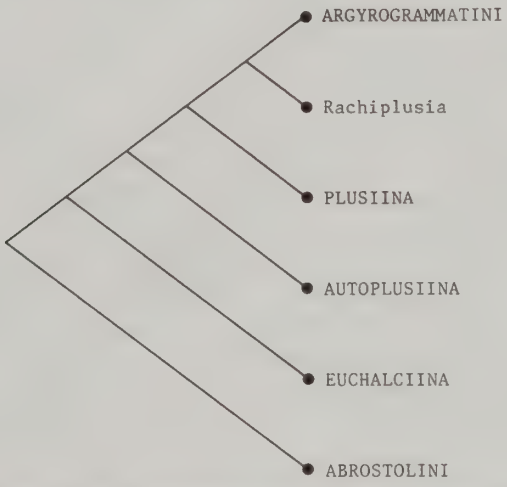


Fig. 26 The branching sequence of the tribes and subtribes on the 647-step cladograms. Note that the position of *Rachiplusia* is the same as on subcladogram 12 of the 648-step cladograms (Fig. 19) but that the Autoplusiina and the Plusiina have exchanged positions.

However, the 647-step cladograms (which, given that the branch-swapping procedure ran to completion, are most likely the shortest for this data set) are based upon the same characters (with one exception) as the previously rejected 648-step subcladogram 12. Both topologies unite the Argyrogrammatini, Plusiina and Autoplusiina using characters 83:0 → 3 and 116, and treat *Rachiplusia* as the sister-group of the Argyrogrammatini based on characters 14:0 → 2 and 110. In addition, the latter relationship is supported on the 647-step cladograms by reversals in characters 18 and 148, both of which are highly homoplasious. Finally, the Plusiina are placed as sister-group to the Argyrogrammatini + *Rachiplusia* solely on the basis of character 162. This character (presence/absence of a subapical cornutus) is also highly homoplasious and was rejected as reliable in connection with the discussion of the relative positions of *Agrapha* and *Plusiopalpa*. Thus, the 647-step minimum-length cladograms can no more be accepted than those 648-step cladograms that include subcladogram 12. Therefore, they are rejected in favour of a longer cladogram but one in which the supporting characters are more reliable.

Evaluation of the preferred cladogram

Following from the decisions reached in the previous two sections, the preferred cladogram (Figs 27, 28) is 648 steps in length and consists of subcladograms 2, 3, 5, 10 and 11; the outgroup topology that places the Stictopterinae closest to the Plusiinae; and the sections held in common by all the alternative 648-step cladograms. The first part of the evaluation of the (preferred) cladogram is character-oriented insofar as the emphasis is placed primarily upon the branches along which a given character changes. Each character will be taken in turn and its character state distribution on the cladogram discussed, with particular

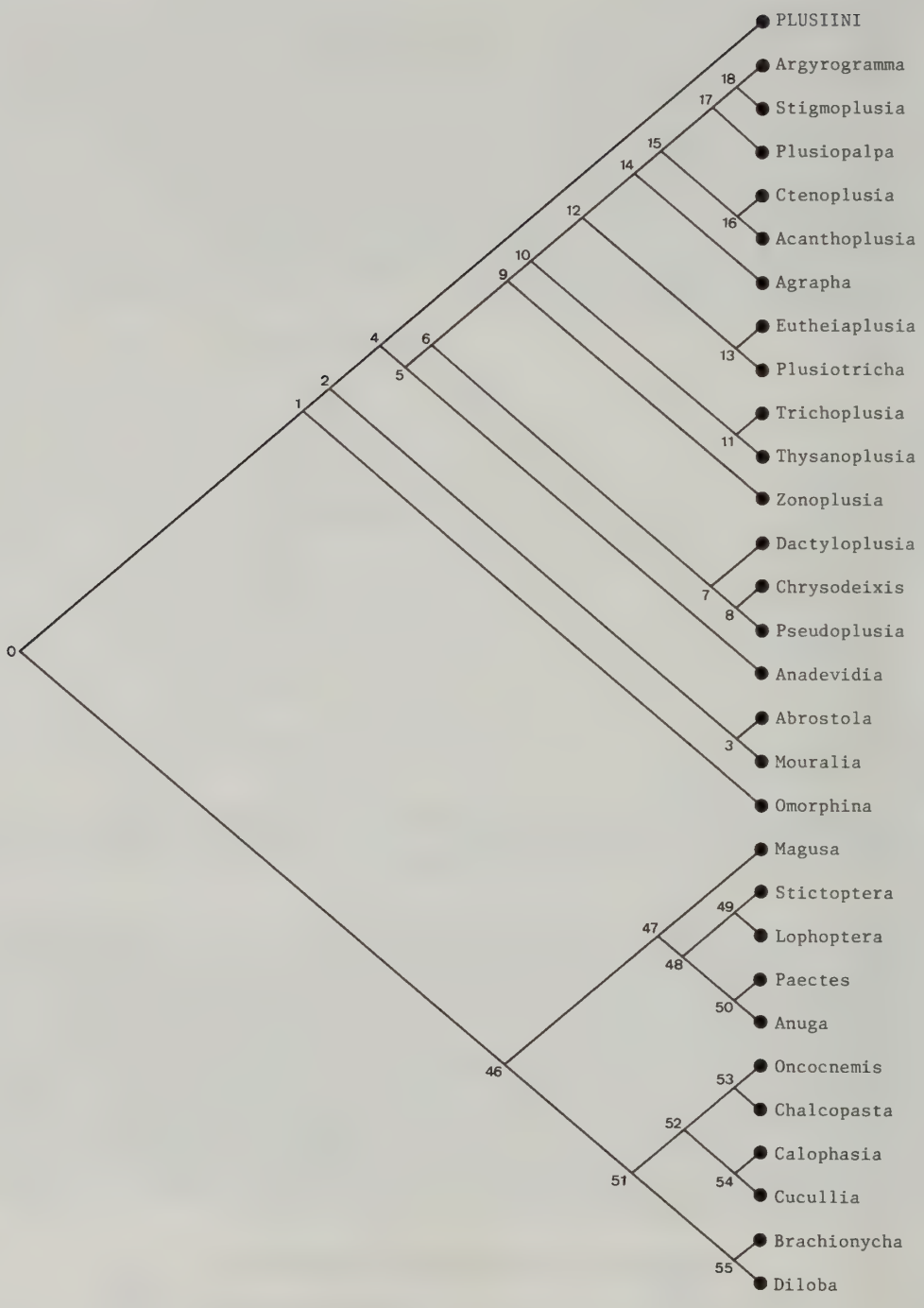


Fig. 27 The preferred 648-step cladogram showing the branching sequence of the outgroups and the Plusiinae except for the Plusiini (see Fig. 28). The numbers on the nodes are the clade reference numbers used to identify clades in the evaluation of characters and taxa.

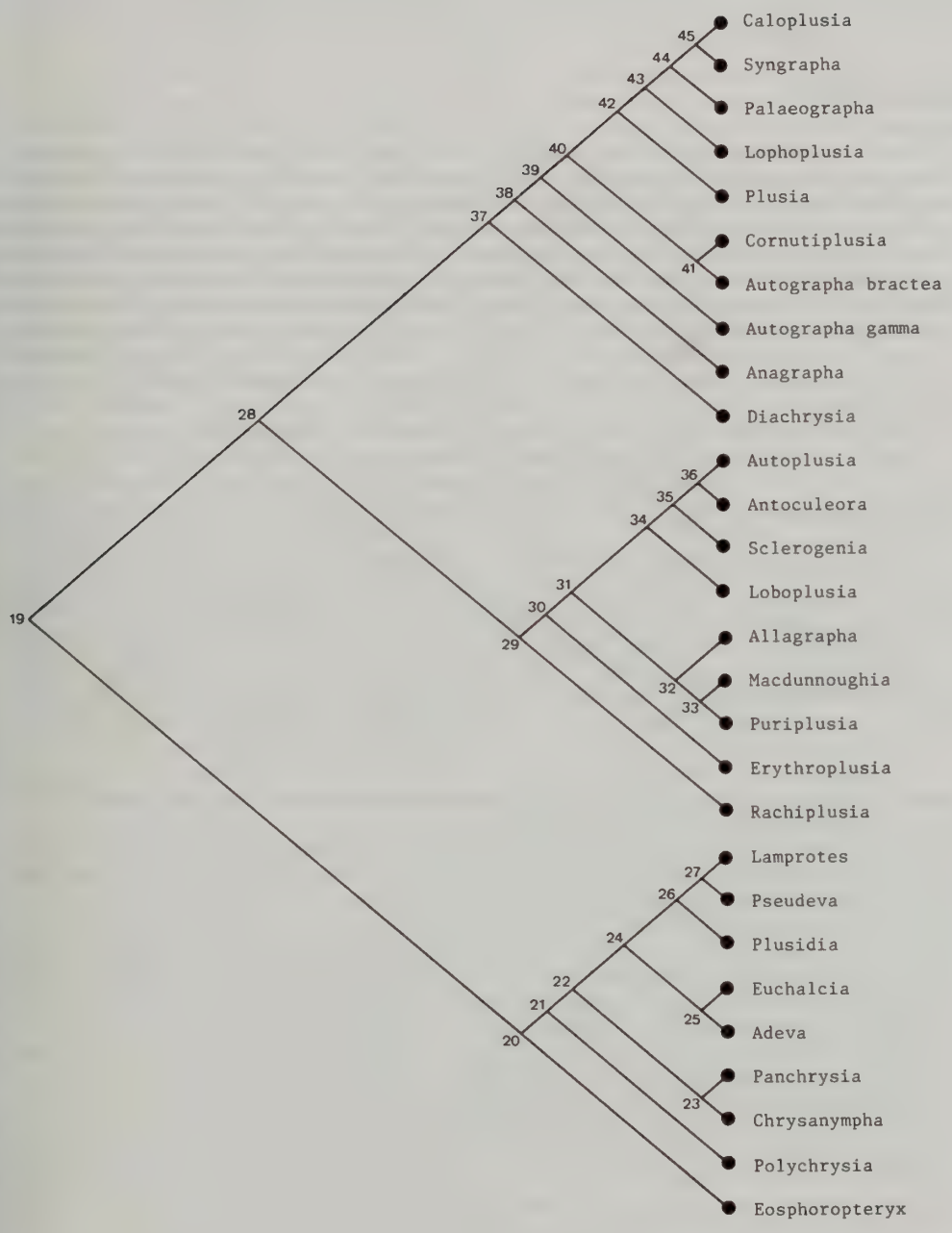


Fig. 28 The preferred 648-step cladogram depicting the branching sequence of the genera of the tribe Plusiini. The numbers are the clade reference numbers.

reference to any homoplasy, alternative optimizations and possible errors in coding and scoring states. The character consistency index (c) of each character is given in parentheses after the character number. The second part of the evaluation is taxon-oriented and examines each of the clades and its supporting characters in turn. The aim here is to determine to what degree each clade may be expected to be corroborated in the light of further data. Clades without formal names are referred to by numbers that are given on the cladograms in Figs 27, 28.

Character analysis

Wing pattern

1 (0·333) The presence of raised scales in the forewing cell is one of the classic Hampsonian noctuid characters. Hampson (1913) noted their occurrence in the Plusiinae in *Abrostola* and *Mouralia*, and also in *Chrysanympha*, the sole species of which he placed in *Abrostola*. Raised scales in *Chrysanympha* were not observed by Eichlin & Cunningham (1978), nor were they in this study. This character state also occurs elsewhere in the Noctuidae, most notably as a defining character for the Sarrothripinae and as a secondary character for distinguishing the Stictopterinae from the Euteliinae. However, in this study, the forewing of *Lophoptera* (Stictopterinae) was found to be smooth, while raised scales were observed in *Anuga* (Euteliinae). As a result, 1 has a low consistency, being convergently derived in the Abrostolini, *Stictoptera* and *Anuga*. It weakly supports the monophyly of the former but more extensive sampling is required to adequately document its occurrence in the Stictopterinae and Euteliinae.

2 (1·000) This character is apomorphic for the Abrostolini. Superficially similar patterns occur elsewhere (e.g. *Paectes abrostoloides* (Guenée)) but lack this element.

3 (0.143) The Y-mark is one of the characteristic elements of the forewing pattern of the Plusiinae. Within the subfamily, it appears to be synapomorphic for the Argyrogrammatini + Plusiini, but with multiple reversals. In some instances (*Anadevidia, Allagrapha*), the lack of a Y-mark appears to be part of a general simplification of the wing pattern, while in others (*Thysanoplusia*, clade 22), it is due to further modification and elaboration of the pattern and possible overlaying of the Y-mark by more derived elements. The latter hypothesis is supported in *Thysanoplusia* by the observation that only *T. intermixta* and a few, apparently closely related, species lack the Y-mark (see character 9), while the remaining species (e.g. *T. indicator* (Walker), *T. daubei*) possess a more typical pattern including a Y-mark, albeit somewhat modified. *Diachrysia* (q.v.) merits further attention because in some species (e.g. *D. leonina* (Oberthür)), the pattern is as simple as in *Allagrapha*, but in others (e.g. *D. chryson*, and more so, *D. chrysitis* and *D. zosimi* (Hübner)), this simple pattern is further elaborated with large areas of golden-green metallic scales (see character 9). Within clade 22, *Lamprotes* appears to have regained the Y-mark. This result suggests that the small golden C-mark in this genus may not be homologous with the Y-mark.

An alternative optimization of character 3, in which the Y-mark is convergently gained in clade 6 (Argyrogrammatini less *Anadevidia*) and the Plusiini, with the lack in *Anadevidia* being treated as plesiomorphic, is rejected as a less satisfactory interpretation.

4 (0.667) State 1 for this character is synapomorphic for the Argyrogrammatini and Plusiini, although there are independent reversals in *Zonoplusia* and *Eutheiaplusia*. State 4, in which the pink line is replaced by a white line, is independently derived from state 1 and is synapomorphic for *Euchalcia* and *Adeva*. There are alternative optimizations for states 2 and 3, the best hypothesising the former state to be a synapomorphy of *Ctenoplusia* and *Acanthoplusia*, with the latter condition being autapomorphic for *Ctenoplusia*. However, state 3 is not universal within *Ctenoplusia*, but may help delimit a subset of this genus including not only *C. limbirena*, but perhaps also such species as *C. melanocephala* (Möschler), *C. micans* (Dufay) and *C. polycampta* Dufay.

5 (0·200) Scattered, individual black scales on the forewing appear to be convergently derived in all the genera that possess them. This was not unexpected for *Erythroplusia*, in which such scales are present in one of the species (*E. rutulifrons*) but absent in the other (*E. pyropia*). In addition, this genus is only distantly related to the other genera that possess these scales, most of which are members of the Euchalciina. Within the Euchalciina, state 1 has been independently gained in *Polychrysia, Chrysanympha, Adeva* and *Pseudeva*, suggesting that the correct homologies have not yet been discovered. Further sampling, however, is unlikely to improve matters. A cursory examination of the other species in the genera concerned showed that black scales were absent entirely in all species of *Panchrysia, Euchalcia* and *Plusidia* (providing *Plusidia imperatrix* Draudt is placed in *Polychrysia*, see below), and present in all *Polychrysia* and *Pseudeva*, although only weakly developed in *P. palligera* (Grote). Scattered black forewing scales can also be seen in the unanalysed *Syngrapha parilis* (Fig. 96).

6 (0·100) The presence or absence of the tornal scale tooth is a highly variable and homoplasious character. Although characteristic of the Argyrogrammatini and Plusiini, it is multiply lost and regained, with numerous alternative sequences of change. One such sequence in clade 4 postulates acquisition followed by subsequent loss in *Agrapha, Anadevidia, Erythroplusia, Loboplusia*, clade 24 and clade 40, with regain in *Palaeographa, Autographa bractea* and *Lamprotes* + *Pseudeva*. The scale tooth is evidently a highly unreliable character.

7 (0·500) Yellow hindwings occur scattered throughout the Plusiinae and seem to be partially correlated with an arctic-alpine habitat. In the taxa under study, they have been independently developed in *Omorphina* and *Syngrapha* + *Caloplusia*. Whilst yellow hindwings are characteristic of the group of species related to *S. devergens* and *C. hochenwarthi* (e.g. *C. tibetana* Staudinger, *S. ignea* (Grote), *S. microgamma* (Hübner), *S. montana* (Packard), *S. parilis* [although this last species has unique white hindwings]), they also appear to have been independently derived (Eichlin & Cunningham, 1978) in another group of syngraphas, which includes *S. diasema* (Boisduval), *S. borea* (Aurivillius), *S. diversigna* Ottolengui, *S. orophila, S. sackenii* (Grote) and *S. snowii* (Edwards). Additional plusiines with yellow hindwings include *Trichoplusia exquisita* (Felder) (Fig. 45), *Panchrysia dives* (Eversmann), *Rachiplusia virgula* (Blanchard) and *Autographa sansoni* Dod. This colour pattern may prove to be of use within *Syngrapha* (s.l.) in a wider study but should be treated with caution.

8 (1·000) A hyaline hindwing base is apomorphic for the Stictopterinae.

9 (0·333) Extensive patches of green-gold scales have been independently acquired by *Chalcopasta, Thysanoplusia* and *Diachrysia*. The former supports Hogue's (1963) contention that this colour pattern is convergent in the stiriines and plusiines. This analysis also demonstrates that the pattern similarity between *Thysanoplusia* and *Diachrysia* is also superficial.

10 (0·500) Similarly, a less pronounced, general metallic sheen on the forewings is also convergent between *Chalcopasta* and the plusiines.

11 (0·333) The black spot at the apex of forewing vein M_3 is interpreted as convergent in *Stigmoplusia, Plusiotricha* and *Pseudoplusia* + *Chrysodeixis*.

12 (0·100) This character, the degree of silver scaling around the reniform stigma, has already been dismissed above, when choosing between subcladograms 5–8, as virtually useless for providing evidence of relationship.

13 (0·500) The loss of the hair-like scales on the forewing cell underside is interpreted as convergent in *Chalcopasta* and the euteliines + stictopterines.

Wing structure

14 (0·600) Three independent transformation series appear to be present in this character, all of which treat the widespread state 0 as plesiomorphic and all of which have alternative sequences of state change. The most parsimonious for each in terms of logical transformations is as follows. Within the Plusiinae, the Argyrogrammatini are characterized by the change $0 \rightarrow 1$, while clade 6 is defined by change $1 \rightarrow 2$. The change $0 \rightarrow 2$ has been convergently derived in *Rachiplusia* and *Autoplusia*. The Stictopterinae + Euteliinae are united by the transformation $0 \rightarrow 3$. There are then two further independent changes: $3 \rightarrow 4$ characterizes *Paectes*, while $3 \rightarrow 5$ is apomorphic for the Stictopterinae. The node uniting *Brachionycha* and *Diloba* can take a value of 0, 2 or 6. An independent origin of state 2 in *Brachionycha* and of state 6 in *Diloba* is supported by the presence of state 0 in *Brachionycha nubeculosa* (Esper), *Psaphida resumens* Walker and *Copivaleria grotei* (Morrison).

15 (0·500) As was expected, the transformation series of reduction in hindwing vein M_2 (the trifine/quadrifine dichotomy) did not emerge non-homoplasious. The plesiomorphic state remains uncertain but the Plusiinae can be delimited by state 1 (although this is convergently derived in *Diloba*, and *Mouralia* possesses state 2); the Stictopterinae + Euteliinae by state 0; and *Calophasia* by state 3. Whatever the eventual outcome, it is certain that the trifine condition will be found to have been attained on several, if not numerous, occasions.

16 (0·250) The apically-produced forewing at vein R_4 is interpreted as convergently derived in *Lamprotes* + *Pseudeva, Panchrysia, Allagrapha* and *Diachrysia*.

17 (0·500) This venational character unites the Stictopterinae and Euteliinae but is reversed in *Paectes*.

18 (0·200) The origin of vein M_2 in the hindwing is partially correlated with character 15 and the development of the trifine condition. It is even more highly homoplasious, with numerous convergences and reversals, which include independent derivations of state 3 from both state 1 and state 2. Many genera appeared intermediate between states 1 and 2 and this character is perhaps best disregarded.

19 (0·200) The apomorphic state for the outline shape of the hindwing has been developed five times

independently in *Mouralia, Panchrysia, Magusa, Calophasia* + *Cucullia* and *Lamprotes* + *Pseudeva*, although the precise condition in *Panchrysia* and *Lamprotes* is unclear. Much of the homoplasy may be due to its partial correlation with character 15.

20 (0·667) The plesiomorphic state for the scale arrangement appears likely to be state 1, with state 2 being a good synapomorphy for the Stictopterinae + Euteliinae + *Magusa*. State 0 is interpreted as convergent in *Omorphina* and *Brachionycha* + *Diloba*.

21 (1·000) The presence of a short distal section of forewing vein *CuP* is synapomorphic for *Brachionycha* and *Diloba*.

Head

22 (0·333) Lashed eyes characterize the Plusiinae and clade 51 of the outgroups, with reversals in *Brachionycha* and *Chalcopasta*. Very long lashes have been independently acquired in *Abrostola, Cucullia* and *Diloba*.

23 (1.000) Bulbous eyes unite the Stictopterinae, Euteliinae and *Magusa*.

24 (0·500) The prominent rim around the eyes has been convergently gained in *Omorphina* and *Syngrapha* + *Caloplusia*. This character is an alternative statement of the 'classic' character 'eye small and elliptical', and has been functionally correlated with a diurnal habit (Hardwick, 1970: 15; see also Kitching, 1984: 184).

25 (1·000) A lower frons that is scaled only at the edge unites the Stictopterinae and Euteliinae.

26 (1·000) Like character 23, character 26, the degree of prominence of the frons, unites the Stictopterinae, Euteliinae and *Magusa*, and may only be an alternative formulation of that character.

27 (0·667) Triangular pilifers are apomorphic for the Plusiinae, although they are convergently derived in *Calophasia*. Broad, reduced pilifers are autapomorphic for *Diloba*.

28 (1·000) A dorsally delimited frons unites the plusiine tribes Abrostolini, Argyrogrammatini and Plusiini.

29 (1·000) A convex occiput is apomorphic for the Plusiinae.

30 (0·500) A narrow frons in the male is interpreted as convergent in *Stictoptera* and *Anuga*.

Proboscis

31 (1·000) A reduction in the number of apical sensilla on the proboscis characterizes the Plusiinae, while an independent total loss unites *Brachionycha* and *Diloba*. This latter condition is probably a direct correlate of the extreme reduction of the proboscis found in these two genera (character 32).

32 (0·667) As referred to above, the proboscis in *Brachionycha* and *Diloba* is very reduced and non-functional. Most outgroup genera have a somewhat short, stout proboscis but in one pair, *Calophasia* + *Cucullia*, it is longer and thinner. This condition is convergent upon that found in the Plusiinae.

33 (0·667) Most outgroup genera have ridged styloconic sensilla apically on the proboscis. In the plusiines, these sensilla are smooth, as they are in *Cucullia*, by convergent derivation. The euteliines are characterized by the further elaboration of three of the ridges into 'wings'. Close examination of the sensilla of *Stictoptera* (Fig. 113) reveals partially-developed 'wings', thus strengthening the hypothesised sister-group relationship between the Stictopterinae and the Euteliinae.

34 (1·000) State 1 for this character unites *Magusa*, the Stictopterinae and the Euteliinae. State 2 is found only in *Brachionycha* and *Diloba* and is functionally correlated with character states 31:0 and 32:2; the lack of apical styloconic sensilla allowing setae to extend to the apex of the reduced proboscis.

35 (1·000) Only in the Plusiinae are the strengthening bars of the proboscis semicircular to the apex. The apical nodules in the euteliines are restricted to the extreme tip of the proboscis and are preceded by very strong semicircular bars. However, these bars appear to be structurally different to those in the Plusiinae and are treated as non-homologous.

36 (1·000) Dense, regular, basal microspines on the proboscis are characteristic of the euteliines.

Labial palps

37 (1·000) Smooth ventral edges to the labial palps unite the stictopterines, euteliines and *Magusa*.

38 (0·500) Although the apomorphic state for this character defines the outgroup clade 51 (less *Oncocnemis* + *Chalcopasta*, in which it is reversed), the semi-erect scales in the four genera concerned are differently distributed and thus possibly not homologous. In *Diloba* and *Cucullia*, semi-erect scales are present on both the inner and outer surfaces; in *Brachionycha*, they are restricted to the inner surface; while in *Calophasia*, they occur only on the outer surface.

39 (0·500) A blade-like labial palp segment 3 is characteristic of the Euchalciina but is reversed in *Euchalcia* + *Adeva*.

40 (0·500) A labial palp in which segment 1 is subequal in length to segment 2 is apomorphic for clade 51 in the outgroups but is reversed in *Calophasia*.

41 (0·250) An elongate labial palp segment 3 is interpreted as having been independently gained within the Euchalciina in *Polychrysia, Chrysanympha* and *Lamprotes* + *Pseudeva*. *Plusiopalpa* also has a superficially similar elongate segment 3 but in this genus, close examination reveals that the elongation is dorso-distal to the VRO (Fig. 157) and so not homologous with the general elongation found in the other four genera, where the VRO remains subapical in position (e.g. Fig. 156).

42 (0·250) An acutely pointed labial palp segment 3 has been independently acquired in *Omorphina, Oncocnemis, Lamprotes* + *Pseudeva* and *Panchrysia* + *Chrysanympha*.

43 (0·500) There are two possible transformation sequences for this character on the cladogram. State 1 can either be independently gained in the Stictopterinae and *Paectes*, or unite the Stictopterinae and Euteliinae, with subsequent reversal in *Anuga*. This latter optimization is favoured by the observation that, while a third stictopterine, *Nigramma*, possesses state 1, a fourth, *Odontodes*, lacks it. Thus, in this slightly larger sample of genera, state 1 would have to be reversed in *Odontodes* (as this genus would form the sister-group of *Lophoptera* rather than be the basal stictopterine lineage; Holloway, 1985), and so it seems more likely that reversal has also occurred in *Anuga*.

44 (0·500) A labial palp segment 3 that is subspherical appears to have been independently derived in *Brachionycha* and in *Chalcopasta* + *Oncocnemis*.

Antennae

45 (0·500) Very long ventral hairs on the antennae have been independently acquired in *Stictoptera* and *Paectes*.

46 (0·667) Asymmetrically bipectinate antennae are characteristic of the Euteliinae, whereas symmetrically bipectinate antennae have independently arisen in *Brachionycha* + *Diloba* and *Lophoplusia*.

47 (1·000) The three states of this character are mutually exclusive to the three groups that have pectinate antennae: *Lophoplusia* (state 1), the Euteliinae (state 0), and *Brachionycha* + *Diloba* (state 2). The remaining genera were coded * and, as a result, the optimization procedure allowed every node in the cladogram between the three groups mentioned to take any value, 0, 1 or 2. Only a more detailed study of antennal morphology will determine whether any (or none) of these states is comparable to the condition found in those genera with simple antennae, and thus which, if any, is plesiomorphic.

48 (1·000) Pectinations that arise basally on each segment may be synapomorphic for *Brachionycha* + *Diloba*. Alternatively, pectinations that arise distally could be apomorphic for a large group of taxa, including the euteliines and plusiines, but are only expressed in a small minority of the included species. Only the discovery of pectinations in a taxon that normally has simple antennae might provide the required information to allow a decision to be made as to which state is plesiomorphic.

External thoracic structure

49 (0·500) A large thoracic crest is apomorphic for the Plusiinae but also occurs in *Chalcopasta*.

50 (0·500) Vertically-held tegulae appear to have been convergently acquired by *Polychrysia* and *Pseudeva*. This was a difficult character to score, and *partially*-erect tegulae occur in other euchalciine genera (*Lamprotes, Plusidia*). More detailed examination may reveal that character 50 defines a much larger group.

51 (1·000) A truncate dorsal tegular arm is apomorphic for the Abrostolini.

52 (0·667) State 2 of this character displays a similar distribution to character 43, except in this instance, the apomorphic state can either unite the Stictopterinae and Euteliinae then reverse in *Stictoptera*, or be independently derived in the Euteliinae and *Lophoptera*. State 1 is autapomorphic for *Omorphina*.

53 (0·500) The colourless, microspinose extension to the ventral tegular arm is convergently derived in *Stictoptera* and *Anuga*.

54 (1·000) Microspines along the inner edge of the ventral tegular arm are synapomorphic for *Calophasia* and *Cucullia*.

55 (1·000) A ventral tegular arm that is produced on a lateral extension of the main tegular body is synapomorphic for *Brachionycha* and *Diloba*.

56 (1·000) A broad marginal flange on the dorsal tegular arm may prove synapomorphic for the

Plusiinae, Euteliinae, Stictopterinae and *Magusa*. However, only *Brachionycha* and *Diloba* truly lack a flange; the members of clade 52 possess a very narrow flange, less than one scale-base wide, and thus further sampling may result in reinterpretation of this character.

57 (1·000) The attachment point of the patagium is drawn out only in the Stictopterinae + Euteliinae.

Legs

58 (0·111) This character posed coding problems for those genera in which the foretibia was striped or mottled (*Chrysanympha, Adeva, Cucullia, Diloba, Magusa, Stictoptera*), or entirely white (*Eosphoropteryx*). These taxa were coded *. This resulted in several alternative sequences of state change in the Euchalciina. Given that the foretibial white spot is frequently lost elsewhere in the subfamily (*Zonoplusia, Allagrapha, Diachrysia, Plusia*), the best optimization assigns state 1 to *Adeva* and independent losses to *Plusidia* and *Euchalcia*. *Chrysanympha* and *Eosphoropteryx* were optimized to bear state 1. In the outgroups, the white spot was convergently acquired by the euteliines and *Chalcopasta*. *Cucullia, Diloba, Magusa* and *Stictoptera* were treated as having state 0.

59 (0·083) The colour of the dorsal surface of the hind tibiae and tarsi is the most homoplasious character in the data, with six gains and six losses, yet with only one ambiguous assignment of state to an internal node. The uniform white colour may have been independently gained by *Omorphina* and the Argyrogrammatini + Plusiini, or gained by the Plusiinae as a whole and lost in the Abrostolini. Convergent gains occur in *Chalcopasta, Cucullia, Calophasia* (following loss in clade 43) and *Autoplusia* (following loss in clade 34). The remaining reversals occur in *Rachiplusia, Pseudoplusia* and clade 9. Many genera proved difficult to code in that they had a generally unicolorous pattern in which the white apices to the segments were still faintly visible: *Trichoplusia, Zonoplusia, Pseudoplusia, Argyrogramma, Agrapha, Adeva* and *Syngrapha*. They were originally coded 0. Had these taxa been coded 1, the homoplasy would actually have been greater by one step. Character 59 is thus best dismissed as containing any reliable information.

60 (0·500) The basitarsal comb on the male hindleg appears at first analysis to be a very labile character that is interpreted as having been multiply acquired and transformed within the Argyrogrammatini. State 1 is present in *Dactyloplusia, Trichoplusia* + *Thysanoplusia* and *Ctenoplusia* + *Acanthoplusia*, as an independent development in each. State 2 occurs as a transformation of state 1 in *Ctenoplusia* and as an independent derivation from state 0 in *Plusiotricha*. This is not improbable because the comb in *Plusiotricha* consists of a single row of about 9 setae, while that in *Ctenoplusia* comprises only two setae (but see below). State 3 in *Argyrogramma* + *Stigmoplusia* also arises *de novo*. However, while two other species of *Stigmoplusia* (*S. allocota* Dufay and *S. acalypta* Dufay) also possess state 3, two other *Argyrogramma* (*A. basigera* and *A. signata*) lack combs entirely. Additionally, while all species of *Agrapha* lack a differentiated comb, in one species (an unnamed species in the BMNH collection; sp. A, see *Agrapha*, Clade analysis), the inner SV row of spines is basally longer and thinner.

For the remaining genera, a more thorough survey was performed. All *Acanthoplusia* species examined (N = 4) agreed with *A. tarassota*. Most *Ctenoplusia species* (N = 30) had a short row of 2–7 setae, agreeing with *C. limbirena* in setal form, if not exactly in number. *C. aenofusa* (Hampson) and *C. phocea* (Hampson) exhibited state 3 and this suggests that these two species may not belong in *Ctenoplusia* but may be more closely related to *Argyrogramma* and *Stigmoplusia*. *C. epargyra* (Dufay) and *C. leucostigma* (Dufay) lack both a tarsal comb and true blade-like setae on the valve (see character 133), and, likewise, perhaps should be excluded. The former owes its place in *Ctenoplusia* (Dufay, 1970*a*) to a superficial similarity to *Ctenoplusia mapongua* (Holland) and *Trichoplusia sestertia* (Fig. 44) (then in 'Plusia' s.l.), while the latter resembles *C. phocea* in habitus. Finally, *C. albostriata* (Bremer & Grey) and *C. subchalybaea* (Walker) (treated as a synonym of the previous species by Holloway, 1985), together with *Trichoplusia oxygramma* and *T. vittata*, also lack a tarsal comb. The first three taxa, however, do bear modified setae along the ventral edge of the valve. Nevertheless, they may not belong in *Ctenoplusia*. If the above anomalous species of *Ctenoplusia* are excluded, then the genus becomes extremely well circumscribed by the form of the tarsal comb. The modified setae may then prove to be synapomorphic for the genera *Ctenoplusia, Acanthoplusia,* [*Eutheiaplusia*] and *Plusiotricha* (see character 133).

Within *Trichoplusia* (N = 29, excluding *T. oxygramma* and *T. vittata*) and *Thysanoplusia* (N = 9), eight species of the former (*T. rectilinea* (Wallengren), *T. sestertia, T. exquisita, T. arachnoides, T. callista* Dufay, *T. photeina* Dufay, *T. dolera* Dufay and *T. gromieri* Dufay) and three species of the latter (*Thy. orichalcea, Thy. florina* (Guenée) and *Thy. viettei* (Dufay)) lack tarsal combs. However, the vagueness of the limits of these genera renders a critical evaluation impossible until a species level cladistic analysis has been undertaken.

Overall, it should not be considered unlikely that tarsal combs will be shown to have evolved two or more times within the Argyrogrammatini, with multiple, independent subsequent losses. Nevertheless, state 3 may prove to be synapomorphic for *Stigmoplusia*, (?part of) *Argyrogramma* and several possibly related species (?*Ctenoplusia aenofusa, C. phocea*), while state 2 may be apomorphic for *Ctenoplusia*, or a large subset thereof.

61 (0·600) State 1 for this character has been acquired independently three times, in the Stictopterinae, *Plusiotricha* and clade 17. The first of these is almost certainly convergent upon the plusiine condition as a result of logical dependence on the following character. Further suppression of the male foretibial spines (state 2) is synapomorphic for *Argyrogramma* and *Stigmoplusia*, while the most extreme modification is autapomorphic for *Argyrogramma*.

62 (1·000) Reduced hind basitarsal spines are apomorphic for the Stictopterinae + Euteliinae, with total loss on the basal half of the segment occurring in the stictopterines. Spines are also suppressed on the other legs in species showing state 2 and this gives rise to a correlated coding for these genera for character 61.

63 (1·000) Spining on the fore and midtibiae was treated separately from that on the hindtibiae (see character 64). Apical spines (state 1) were autapomorphic for *Rachiplusia*, while extensive spining (state 2) was autapomorphic for *Caloplusia*.

64 (0·429) Spines on the inner surface of the hindtibia are autapomorphic for *Mouralia* and form a separate transformation series from that concerning spines on the outer surface. Most instances of the latter appear to have been independently derived: state 1 in *Autoplusia, Cornutiplusia* and clade 44; state 2 in *Anagrapha* and *Rachiplusia*. Only in *Caloplusia* is state 2 derived from state 1. However, as mentioned above, occasional spines may be observed in *Plusia* and *Autographa*, and so may prove apomorphic for the more extensive clade 38, with multiple subsequent suppression. Also, in *Autoplusia*, one leg of the male *A. egena* examined showed state 2, while the other leg, together with both legs of the female, displayed state 1. Thus this character is also plastic in *Autoplusia*. Overall, the expression of character 64 is variable and should be treated with extreme caution when assessing degrees of relatedness.

65 (0·750) The three forms of SD and D setae on the tarsi have been independently derived; state 1 in *Diachrysia*, state 2 in *Polychrysia*, and state 3, convergently, in *Panchrysia* and *Lophoplusia*.

66 (1·000) Hindlegs are shorter than midlegs only in the Stictopterinae + Euteliinae.

67 (0·500) Ventral lobes on the claw are convergently absent in *Oncocnemis* and *Diloba*.

68 (0·667) Elongate hindleg inner apical spurs occur in the Stictopterinae and Euteliinae. Two sequences of character state changes are possible. States 1 and 2 can be independently derived in *Stictoptera* and the euteliines respectively (the latter *via* state 1); or state 1 can unite the two subfamilies with a transformation to state 2 in the euteliines and a reversal to state 0 in *Lophoptera*. Further sampling within these two subfamilies is required in order to decide between these two competing transformation series.

69 (0·500) Foretibial claws have been independently derived in *Brachionycha* and *Oncocnemis* + *Chalcopasta*.

Internal structure of the prothorax

70 (1·000) A posteriorly recurved prothoracic furca characterizes the Euteliinae + Stictopterinae.

71 (0·500) A ridge on the dorsal edge of the epimeron is convergent between the Euteliinae and *Brachionycha* + *Diloba*.

Male abdomen A1–7

72 (0·500) The narrowly tapered abdomen occurs in *Stictoptera* and the euteliines. As for character 17, this distribution can be accounted for by a gain followed by a loss, or by two independent gains.

73 (1·000) State 3 forms an independent transformation, characterizing the Stictopterinae + Euteliinae. There is some ambiguity regarding the fitting of states 1 and 2. The most morphologically parsimonious sequence treats state 1 as apomorphic for the Plusiinae less the Omorphinini, in which the ventro-lateral edges of the internal flange on A2 are expanded internally. This condition is retained in the Abrostolini, but in the higher Plusiinae (clade 3), the lobes of the flange are even more highly developed, meeting medially but with a ventral notch.

74 (1·000) Internal longitudinal flanges on St2 are autapomorphic for the Euteliinae. Holloway (1985) stated that these structures may be correlated with the resting position of the adults, in which the wings are longitudinally folded and the abdomen is recurved dorsally.

75 (1·000) Components of the trifine hair pencils are found, in this study, only in *Cucullia* and *Magusa*, where they are interpreted as independently derived. Far more taxa need to be examined before any

meaningful information can be extracted from this frequently highly labile (Birch, 1972*b*) character complex.

76 (1·000) Postero-lateral sclerotizations on St7 are apomorphic for clade 6 – the Argyrogrammatini less *Anadevidia*. They are only just discernible in *Pseudoplusia* and *Eutheiaplusia*, a condition that may be correlated with the reduced hair pencils and subdorsal tufts of these genera (see below).

77 (0·429) The presence of dorso-lateral hair tufts on segments A5–7 characterizes clade 6, with independent losses in *Zonoplusia* and *Pseudoplusia*. Additional tufts on segments A(2–)4 are synapomorphic for the members of clade 12, but with subsequent loss in *Acanthoplusia* + *Ctenoplusia*. The presence of distinct additional tufts on A4 is autapomorphic for *Chrysodeixis*. As alluded to above, it may eventually be possible to subdivide state 2 and extract more information, whence further resolution within the Argyrogrammatini may be forthcoming.

78 (1·000) As was originally suspected, the three forms of enclosed hair tufts on A7 are independently derived in *Dactyloplusia* (state 1), *Ctenoplusia* (2) and *Argyrogramma* (3).

79 (1·000) This character (distinct edges to the tufts on A5 and A6) has been discussed earlier in connection with the decision between subcladograms 1 and 2.

Male St8 and ventral hair pencils

80 (0·600) This character is now shown to consist of at least two independently derived forms of hair pencil. State 3 characterizes the Stictopterinae + Euteliinae + *Magusa*, but is also found in *Calophasia* + *Cucullia*. The hair pencils coded by states 1 and 2 are restricted to the Plusiinae. The former unites the members of clade 2 (the Plusiinae less *Omorphina*), while state 2 has been independently derived in *Dactyloplusia* and the argyrogrammatine clade 10. There is some evidence to suggest that the conditions of St8 found in *Zonoplusia, Pseudoplusia* and *Chrysodeixis* may eventually be recognized as reduced forms of state 2, whence this feature would become apomorphic for clade 6. Several other taxa also show partial reductions of the hair pencils and St8.

81 (1·000) The plesiomorphic state for the stictopterine type of hair pencil is interpreted as state 3. This causes some problems in the optimization of states on the internal nodes of the outgroups because *Brachionycha, Diloba, Chalcopasta* and *Oncocnemis* all lack any type of hair pencil and were coded *. However, given the ambiguity in the outgroup relationships and their relatively distant affinities, this is not a serious uncertainty in the current study. Within clade 47, state 0 is probably plesiomorphic, with states 2 and 1 being autapomorphic for *Magusa* and *Anuga* respectively. Given that *Magusa* may not represent the immediate sister-group of the Stictopterinae + Euteliinae (see clade 47, Clade analysis), this sequence of state transformation seems more prudent than the alternatives.

82 (1·000) Similarly, character 82 does not apply to clades 53 and 55. Thus state 0 is apomorphic for *Calophasia* + *Cucullia*, and state 1 for clade 47. State 2 is autapomorphic for *Stictoptera. Anuga*, coded *, is predicted to have state 0.

83 (0·313) This character, the degree of development of the male sternal hair pencils, proved, as expected, to be highly homoplasious, with numerous alternative character state optimizations. The sequence chosen assumed that state 0, as seen in *Abrostola*, is plesiomorphic for the Plusiinae (less *Omorphina*). The large single pocket (state 5) of *Mouralia* is autapomorphic within the Abrostolini. The initial transformation 0 → 3 (well developed, separate pockets) characterizes the Argyrogrammatini + Plusiini. Within the Plusiini, the pockets are reduced to state 0 again in the Euchalciina. This confirms that state 0 in this subtribe is the result of secondary loss and is not due to plesiomorphic absence, as in *Abrostola, providing* that hair pencils have not been independently gained in the Argyrogrammatini and Autoplusiina + Plusiina. A change to state 2 (partially fused pockets) characterizes clade 30 (the Autoplusiina less *Rachiplusia*) but with a reversal to state 3 in *Autoplusia* itself. The Plusiina are characterized by the change 3 → 1 (reduction of pockets to slight invaginations), with independent reversals to states 3 and 0 in *Plusia* and *Syngrapha* respectively.

The situation is less simple in the Argyrogrammatini. A parallel change to state 2 (as in clade 30) occurs to unite the members of clade 6. Within clade 8, there are independent transformations to states 0 and 5 in *Pseudoplusia* and *Chrysodeixis* respectively. The form of the hair pencil is then even more highly modified in the more derived members of the latter genus, as outlined above (Terminology). State 4 (fused pockets) is apomorphic for clade 17, with a reversal to state 3 in *Stigmoplusia*. There are also parallel changes from state 2 to state 3 in *Acanthoplusia* and *Trichoplusia* + *Thysanoplusia*.

The sternal hair pencils are obviously highly variable and maybe labile structures. However, the distribution of states and homoplasy is very far from random and more extensive sampling could result in this complex proving very useful.

84 (0·250) A sclerotized bar on the hair pencil pockets is apomorphic for clade 10 but with subsequent independent losses in *Plusiopalpa, Acanthoplusia* and *Thysanoplusia*.

85 (1·000) Differentiated hair pencil insertions are synapomorphic for *Argyrogramma* and *Stigmoplusia*.

86 (0·333) As discussed above, accessory pockets on the preferred cladogram must be developed in clade 14 but then independently lost in *Plusiopalpa* and *Ctenoplusia*.

87 (0·500) Short, outer scales on the hair pencils also characterize clade 14, but with a reversal in clade 17.

88 (0·500) Long inner tufts of hair pencil scales are convergently derived in *Agrapha* and *Argyrogramma*.

89 (1·000) Secondary hair brushes are synapomorphic for the members of the Argyrogrammatini.

90 (1·000) An anterior flange on the lateral arms of St8 is restricted to *Argyrogramma* and *Stigmoplusia*.

91 (0·500) Lateral arms of St8 that twist dorsally over the hair pencils are apomorphic for the Argyrogrammatini less *Anadevidia*, but the change is reversed in *Pseudoplusia*, which also has much reduced hair pencils. Further, the development of a deep basal concavity characterizes clade 12 but with subsequent reversal in *Plusiopalpa*.

92 (0·750) This character was also discussed in detail above, with regard to subcladograms 1 and 2. State 1 is convergently derived in clade 12 and *Dactyloplusia*; state 3 is apomorphic for clade 14 and this transforms to state 2 to unite *Argyrogramma* and *Stigmoplusia*.

93 (0·600) The form of fusion of the apices of the dorsal arms of St8 is fairly homoplasious. State 2 (in which the arms fuse into a rounded apex) is apomorphic for clade 10, with further transformations to state 3 (transversely oriented dorsal arms), uniting *Argyrogramma* and *Stigmoplusia*, and state 1 (converging dorsal arms), autapomorphic for *Thysanoplusia*. However, state 1 occurs outside clade 10 in clade 7, with a reversal to state 0 in *Pseudoplusia*. This character has probably not been coded correctly and further sampling of taxa may clarify matters. The form of St8 will almost certainly prove to be highly important in the future critical resolution of the interrelationships of the taxa within the Argyrogrammatini.

94 (0·750) There are several alternative optimizations for the internal node states for this character too. The most probable, on present evidence, interprets state 2 (presence of broad, flat, 'greasy'-looking scales ventrally between the dorsal arms of St8) as apomorphic for clade 6. There are subsequent transformations to state 3 (scales fused into a flat plate) in *Argyrogramma* + *Stigmoplusia*, to state 0 (a reversal) in *Pseudoplusia*, and to state 1 (broad, erect, spatulate scales) in *Chrysodeixis* (which is further modified in the more derived species of this genus; see above). Superficially similar scales to those in *Chrysodeixis* occur in *Anadevidia*, but in the latter genus, they were interpreted as the scales of the secondary hair brush. Thus they are convergent upon the condition found in *Chrysodeixis*, which bears normal secondary hair brushes in addition to the apical spatulate scales.

95 (0·500) Long, fine scales ventrally between the lateral arms of St8 characterize clade 30, although they are subsequently lost in *Sclerogenia*.

Male genitalia – uncus, tegumen & anal tube

96 (0·500) A ventrally flattened uncus is considered to have arisen independently in *Paectes, Calophasia* and *Brachionycha* + *Diloba*. State 2, a subspherical uncus, is autapomorphic for *Anuga*.

97 (0·250) A straight uncus has been derived independently four times: *Chalcopasta, Chrysodeixis, Stigmoplusia* and clade 44.

98 (0·500) The uncus has become distally dilated dorsally independently in *Agrapha* and *Argyrogramma*.

99 (1·000) A notch between the tegumen and uncus is characteristic of the Plusiinae less the Omorphinini. A further production of the tegumen apex unites *Allagrapha, Macdunnoughia* and *Puriplusia*.

100 (1·000) A concave base to the uncus is an apomorphy of the Abrostolini.

101 (1·000) A tegumen with a distinct angle is synapomorphic for the members of the Euchalciina. The apomorphic state is weak in *Panchrysia* and *Pseudeva*, and present in only one of the two *Euchalcia* specimens examined.

102 (1·000) An uncus that is medially flattened and expanded is apomorphic for the Abrostolini.

103 (1·000) The presence of a distinct median suture on the uncus is also apomorphic for the Abrostolini.

104 (0·500) Widely divergent tegumenal arms are convergently derived in *Antoculeora* and *Erythroplusia*.

105 (0·111) The origin of the anal tube with respect to the LASTs and uncus base is highly homoplasious.

This character seems generally to be correlated with the overall dorsal appearance of the tegumen apex, LASTs and uncus base. There is a general trend, which is difficult to quantify, that as the anal tube moves anteriorly, the apex of the tegumen becomes elongate and the outline of the tegumen → LASTs → uncus smoothes out. Until such time as the morphology of this complex region is clarified, the best optimization for the development of the apomorphic state may be to postulate independent gain wherever possible. Thus, state 1 may have arisen separately in *Chalcopasta*, clade 38 (with reversal in *Plusia*), *Anadevidia, Agrapha, Argyrogramma, Trichoplusia* and clade 7. In the last of these, the anal tube of *Chrysodeixis chalcites* arises at the uncus base but this condition appears to be the end product of a reversal series. The 'plesiomorphic' species, *C. argentifera*, has an anterior origin of the anal tube (state 1), as in *Dactyloplusia* and *Pseudoplusia*, while the 'intermediate' *C. illuminata* shows an intermediate position. The 'derived' *C. kebea* (and *C. chalcites*), as defined by an arrowhead-shaped St8 (see Terminology), have reverted totally to the plesiomorphic condition for character 105.

106 (0·500) The fusion of the LASTs to the underside of the tegumen has occurred independently in the Argyrogrammatini + Plusiini and in *Chalcopasta*.

107 (0·200) Subdorsal bars on the anal tube have been gained on several occasions: *Chrysanympha, Lophoplusia*, the Abrostolini, and clade 47 (with subsequent loss in the euteliines). Within the latter, an alternative optimization hypothesises independent gain in *Magusa* and the stictopterines. However, extreme modification of the LASTs in *Paectes* and their complete absence in *Anuga* suggests that loss of the bars in the euteliines is a more satisfactory hypothesis.

Male genitalia – vinculum & pleurite

108 (0·125) The presence of a ventral tooth on the vinculum is also a highly homoplasious character state. It has been acquired by clade 39 (with no reversals). *Erythroplusia, Sclerogenia* and the Argyrogrammatini. Within the latter, the tooth has been lost four times, in clades 7 and 13, and in *Acanthoplusia* and *Argyrogramma*. The tooth represents the insertion point of the S2 muscle (Bayer, 1965), which, together with other muscles, retracts the genitalia into A8. Bayer noted the absence of S2 in *Chrysodeixis acuta*, a species that also lacks a tooth. Thus, an extensive investigation of genital musculature, and its correlation with the presence/absence of the vincular tooth, might help clarify the homoplasy exhibited by character 108. (For an alternative musculature nomenclature, see Tikhomirov, 1979.)

109 (0·333) A vinculum that is S-shaped in lateral view has been independently gained in clades 21 (weakly expressed) and 39 and in *Cucullia*. Since the S1 muscle inserts dorso-apically on the vinculum (Bayer, 1965), this shape could also be functionally correlated with the musculature for retracting the genitalia.

110 (0·200) A Y-shaped vinculum has been convergently derived in *Paectes, Rachiplusia* and clade 6 (with subsequent reversal in *Dactyloplusia* and *Trichoplusia*). This character is relatively trivial and probably of low importance.

111 (0·500) An attenuated spine-like vinculum is apomorphic for *Chrysodeixis* + *Pseudoplusia*. *Stigmoplusia* has a produced vinculum but with a rounded apex, a condition shown here to be non-homologous.

112 (0·750) Dorso-lateral emarginations (state 1) of the vinculum arms have been independently acquired by *Thysanoplusia* and clade 14. Within the latter, the emarginations are expanded into sharp points (state 2) in *Stigmoplusia*. The blunt hooks (state 3) of *Plusiotricha* represent an independent, non-homologous derivation from state 0.

113 (0·333) A broad, flat, cone-like vinculum is regarded as apomorphic for the members of clade 31 but is reversed in the included clade 35. It is also independently derived in *Anagrapha* (but see Clade analysis).

114 (0·500) A flattened, entire, conical vinculum is convergently derived in *Rachiplusia* and the stictopterines + euteliines. Originally scored *, *Stictoptera* was optimized to possess state 1. This suggests that further work in the Stictopterinae should show the condition in this genus to be derivable from state 1.

115 (1·000) Distally convergent vinculum arms are apomorphic for the Euteliinae.

116 (0·333) A distinct, sharp, basal notch on the pleurite is apomorphic for the Autoplusiina + Plusiina, although it is convergently present in *Anadevidia* and reversed in *Antoculeora*. The latter condition was commented upon above, when discussing the position of *Rachiplusia* and the branching sequence of the subtribes of the Plusiini, and is interpreted as being correlated with the highly modified male genitalia found in *Antoculeora* (see also characters 117 and 118).

117 (0·500) A broad, flat lateral flange on the pleurite is considered to be an apomorphy of the Plusiini.

Like character 116, the apomorphic state is lost in *Antoculeora*. According to Bayer (1965), this flange represents the insertion point for the genitalia retraction muscle S3.

118 (0·667) State 1, in which the pleurite lies along the antero-dorsal edge of the tegumen, is interpreted as plesiomorphic. State 2, where only the apex of the pleurite is in contact with the tegumen, is autapomorphic for *Antoculeora*, while *Magusa* and *Calophasia* appear to have independently acquired state 0, in which the apex of the pleurite articulates on the inner edge of the tegumen in a pocket. However, * codings for *Diloba*, the stictopterines and the euteliines render this conclusion open to question.

119 (0·500) Partial fusion of the pleurite and VAVB has convergently arisen in *Plusiotricha* and *Ctenoplusia* + *Acanthoplusia* (but see characters 60 and 133, and Clade analysis).

120 (1·000) A very narrow pleurite closely appressed to the antero-dorsal edge of the tegumen is synapomorphic for *Chrysodeixis* and *Pseudoplusia*.

121 (0·500) The three states of this character are treated as independent derivations, all of which occur twice. A very short or missing VAVB (1) characterizes the Plusiini and Stictopterinae. A VAVB modified into a blunt lobe (2) arose convergently in *Abrostola* and *Argyrogramma*. In *Calophasia* and *Oncocnemis*, the VAVB is missing and the tegumen base is produced below the pleurite to approach the vinculum apex (3).

122 (1·000) Socii are apomorphic for the euteliines.

123 (0·500) Complete fusion of tegumen and vinculum arms has, as suspected *a priori*, occurred in independently in *Diloba* and the Stictopterinae + Euteliinae.

Juxta & anellus

124 (1·000) The apex of the juxta is fused to the aedeagus ventrally only in the Abrostolini.

125 (1·000) Apical thickening of the juxta is also apomorphic for the Abrostolini.

126 (1·000) Fusion of the juxta, by a bar, to the inner edge of the sacculus near the base of the clavus occurs only in the Abrostolini.

127 (0·429) A parallel-sided notch has developed apically on the juxta three times in the Plusiinae; in *Omorphina, Chrysodeixis* and the Plusiini. Within the latter, it has been lost in *Allagrapha* and independently modified into a subapical process twice, in *Anagrapha* and clade 44. The further elaboration of this process into a sharp spine is synapomorphic for *Syngrapha* and *Caloplusia*. Although the character is homoplasious overall, state 3 may allow some resolution within *Syngrapha* (s.l.). The sharp spine is present only in a subset of those species with yellow hindwings (see character 7) allied to *S. devergens* and *Caloplusia hochenwarthi*: *S. ignea, S. microgamma*, and *S. alticola*. The spine is absent in *S. montana* and represented by a 'strong point, but not a distinct, sclerotized spine' in *S. parilis* (Eichlin & Cunningham, 1978). However, similar structures occur elsewhere; *S. angulidens* (Smith) has a sharp apical point, *S. sackenii* shows a similar structure to *S. parilis*, and many other species exhibit a weak, blunt projection. Nevertheless, used with caution, the form of the juxta apex should prove useful in elucidating relationships within *Syngrapha* and maybe the Plusiina as a whole.

128 (0·400) A scobinate juxta apex is apomorphic for clade 7, with distinct thorns autapomorphic for *Pseudoplusia*. State 1 has also been independently derived in *Thysanoplusia* and, as initially suspected, *Plusiopalpa* and *Cucullia*.

129 (1·000) A weakly sclerotized, crescentic juxta is autapomorphic for the Euteliinae.

130 (0·333) For this character, the outgroups were all coded *. The plesiomorphic state in the Plusiinae was interpreted to be state 1, in which the juxta is fused to the saccular flanges. The juxta has become free three times independently, when saccular flanges are also present, in *Agrapha, Pseudoplusia* + *Chrysodeixis* and *Argyrogramma* + *Stigmoplusia*. Interestingly, all those plusiine taxa that lack saccular flanges (Abrostolini, *Trichoplusia, Autoplusia*) were optimized to display state 1 – juxta fused to flanges! This result suggests that a recoding of this character, incorporating the next (q.v.), will be necessary if any sense is to be made of the feature in future studies.

Male genitalia – valve

131 (0·250) The presence of saccular flanges characterizes the Plusiinae, with independent losses in the Abrostolini, *Trichoplusia* and *Autoplusia*. The implication for the previous character is that, had saccular flanges not been lost in these taxa, then they would have been fused to the juxta.

132 (1·000) The presence of a rounded lobe between the valve bases, formed from the fused saccular flanges, is synapomorphic for *Panchrysia* and *Chrysanympha*.

133 (0·500) Blade-like setae are interpreted here as convergently derived in *Ctenoplusia* + *Acanthoplusia* and *Plusiotricha*. As noted above (character 60), there appear to be problems regarding the

homologies of this and similar setal modifications. In the present context, the setae coded by state 1 are strongly sclerotized, regularly arranged in a single row along the ventral edge of the valve and shaped like short, broad, curved blades. In *Ctenoplusia albostriata* and *Trichoplusia oxygramma* (McDunnough, 1944), the ventral valval setae are weakly sclerotized and narrow, and thus may not be homologous with the setae found in typical ctenoplusias. Further work is necessary to decide whether this group of species truly belongs in *Ctenoplusia* or represents, say, the sister-group of *Ctenoplusia* (+ other genera?). Similarly, *C. epargyra* and *C. leucostigma* only have spiniform hairs on the ventral edge of the valve, which, in conjunction with their lack of a tarsal comb, argues for their exclusion from the genus. The setae in *C. phocea* are also weak and narrow. Additionally, they are in multiple rows basally, unlike other *Ctenoplusia* species. *C. phocea* also has a tarsal comb consisting of multiple rows of setae (60:3), an elongate vinculum (111:1) but with a rounded apex, and moderately strong dorso-lateral emarginations on the vinculum arms (112:1), strongly suggesting a relationship with *Stigmoplusia*. Finally, *C. aenofusa* is enigmatic. It has highly modified and autapomorphic setae along the ventral edge of the valve. They are strongly sclerotized and in a single row. However, the distal setae are narrow and strongly angled, while the basal setae are apically spatulate. Also, the setae on the basal half of the sacculus are borne on small marginal projections, unlike most ctenoplusias. As stated above, the tarsal comb is of the form found in *Argyrogramma* and *Stigmoplusia*, and *C. aenofusa*, too, may have its true affinities with these genera.

All *Acanthoplusia* species possess blade-like setae. Dufay (1970*b*) and Holloway (1985) state that these are missing in *A. vermiculata* Dufay, but recessed scale bases along the ventral edge of the valve, typical of *Ctenoplusia* and *Acanthoplusia* (and also *Plusiotricha*), are visible in the holotype. It must be assumed that the blade-like setae, which are often caducous in many species, have been accidentally removed before or when the specimen was prepared and mounted.

Two other genera in clade 14 have modified valval setae. In *Stigmoplusia*, although the type species lacks such setae, three other species (*S. allocota, S. acalypta, S. megista* Dufay) all possess single, short, conical, somewhat flattened setae apically on the valve digitations. In *Agrapha*, the ventral edge of the valve is dorso-ventrally flattened and covered with a dense mat of short, upright, curved, flat scales.

There is obviously a great deal of useful information in these valval setae within clade 12 but an exhaustive species-level analysis will be necessary to extract the maximum information.

134 (1·000) A spatulate lobe arising from the sacculus is autapomorphic for the Abrostolini.

135 (0·500) A uniseriate corona has been convergently derived in *Magusa* and clade 52.

136 (0·500) The presence of basally-directed setose scales on the valve apex is synapomorphic for the Argyrogrammatini. Similar scales in *Mouralia* are interpreted as convergently derived. In *Anadevidia peponis*, the valval setae are extremely persistent and very numerous. However, basally-directed scales are present in *A. hebetata* (Butler) (Chou & Lu, 1978: fig. 2), in the position occupied by the caducous setae of the other argyrogrammatine genera, whereas no such setae occur anywhere in the Plusiini.

137 (0·500) Setae arising from ventral marginal prominences on the valve are interpreted as apomorphic for clade 32, but with an independent derivation in *Omorphina*.

138 (0·500) A spatulate apex (cucullus) to the valve is treated as synapomorphic for the members of clade 12 but with reversal in clade 17. The weak nature of the subapical constriction in *Eutheiaplusia*, together with weak narrowing in *Trichoplusia, Thysanoplusia, Dactyloplusia* and *Pseudoplusia*, suggests further sampling may reveal a very gradual transformation series leading from an unconstricted valve to the extreme condition seen in *Ctenoplusia*.

139 (0·500) The clavus base is obscured by an overfold of the sacculus in *Rachiplusia* and clade 32 convergently.

140 (1·000) A broad, blunt point on the ventral edge of the valve unites *Plusiotricha* and *Eutheiaplusia*.

141 (0·250) The saccular spine is convergently derived in *Diloba* and clade 30, but within the latter, it has been lost in *Autoplusia* and *Loboplusia*. The absence in *Autoplusia egena* is almost certainly a true loss (rather than plesiomorphic absence) since the spine is present in both *A. olivacea* and *'Syngrapha' gammoides*.

142 (0·333) A saccular sheet, in some form, is characteristic within the Plusiinae of clade 31, although it has subsequently been lost in *Loboplusia*. Further modification to form a hook unites *Sclerogenia, Autoplusia* and *Antoculeora*. Convergent occurrences of an apical saccular process appear in *Lophoptera, Calophasia* and *Magusa*.

143 (0·500) The form of the clavus (characters 143–145) is highly homoplasious. Its presence on a distinct peninsula (state 3) is probably plesiomorphic for the Plusiinae. The peninsula is convergently lost in the Abrostolini and *Anagrapha*, so that the dorsal and ventral margins of the clavus are more

or less level (state 2). However, this state arose *de novo* from state 0 in *Cucullia*. The clavus is further modified into a broad lobe in *Abrostola*, but this is convergently derived from an unmodified saccular margin in *Chalcopasta* + *Oncocnemis*.

144 (0·133) This character, the degree of development of the clavus in the Plusiinae, was that used by McDunnough (1944) to subdivide the subfamily into three genus groups. The more extensive sampling of genera of the present study has shown this view to be far too simplistic. A fully developed, tubular clavus (state 0) is interpreted as plesiomorphic, because it is the form that occurs in the only outgroup with a distinct clavus (*Cucullia*). Multiple, independent reduction seems to be the rule, but some reversals (i.e. clavi becoming longer and better developed) do occur. Reduction to a short tubular clavus has occurred in the Argyrogrammatini, clades 24 and 43, *Anagrapha, Loboplusia, Stigmoplusia* (after a reversal in clade 15, see below) and *Omorphina*. Further reductions to a setose bump have taken place in clade 26, *Lophoplusia, Plusiotricha* and *Agrapha*. Reversal from state 2 to 1 occurs only in *Lamprotes*, or alternatively (and this, surprisingly, is the only internal node state ambiguity), state 2 could have arisen independently in *Plusidia* and *Pseudeva*. However, as *Lamprotes* exhibited a clavus form somewhat intermediate between states 1 and 2 (see Characters), this is not too problematical. Reversals from state 1 to 0 occur only in the Argyrogrammatini but thrice, in *Pseudoplusia* + *Chrysodeixis*, *Trichoplusia* + *Thysanoplusia* and in clade 15. As seems to be true of all the widely quoted 'classic' key characters (see also, for example, characters 6, 15 and 64), the form of the clavus is highly unreliable as an indicator of cladistic relationship.

145 (0·333) An elongate, flattened peninsula has been convergently derived in *Erythroplusia, Macdunnoughia* + *Puriplusia* and *Antoculeora*. Interestingly, however, all four of these genera are members of the Autoplusiina.

146 (1·000) A blade-like valve is apomorphic for the Plusiina.

147 (0·500) More or less oval valves are apomorphic for clade 21 of the Euchalciina but also occur convergently in *Omorphina*.

148 (0·200) The presence or absence of the harpes is also very homoplasious, with presence being interpreted as plesiomorphic. Five independent losses appear to have occurred, in the euteliines, *Stictoptera, Rachiplusia, Anadevidia* and clade 34. An alternative optimization in clade 48 hypothesises loss as uniting the Stictopterinae and Euteliinae, with a subsequent regain in *Lophoptera*.

149 (0·250) It was suggested *a priori* that the various forms of inwardly-pointing hooked harpes would prove to be convergently derived and therefore probably non-homologous. This result was obtained, with independent derivations occurring in clade 44, *Trichoplusia, Dactyloplusia* and *Agrapha*.

150 (1·000) Inwardly-curving hooked harpes are apomorphic for *Macdunnoughia* and *Puriplusia*, with further development of a basal, shorter, upcurving hook autapomorphic for the former genus. Interestingly, *Macdunnoughia crassisigna* (Warren) shows an intermediate condition in which the second hook is represented by a small sharp point.

151 (1·000) Deeply cleft valves are autapomorphic for the Stictopterinae.

152 (1·000) Trapezoid valves are autapomorphic for the Euteliinae.

153 (1·000) Valves that, when closed, lie ventrally or subventrally are synapomorphic for the Euteliinae and Stictopterinae.

154 (0·333) Transtillae that are fused and produced posteriorly to a broad, blunt point are convergently derived in *Rachiplusia* and clade 22 (with reversal in the included clade 26).

155 (0·500) Bifurcate transtillae, discussed earlier in connection with the position of *Loboplusia*, are hypothesised to have arisen independently in *Erythroplusia* and *Sclerogenia*.

Male genitalia – aedeagus

156 (0·500) A thin, small aedeagus is apomorphic for clade 47 but reversed in *Paectes*.

157 (0·667) A bulbous coecum (state 2) is synapomorphic for the Plusiini and Argyrogrammatini. In the latter tribe, the coecum can become very enlarged (e.g. 'Plusia' *megaloba* Hampson [Holloway, 1985: 300]; *Ctenoplusia aenofusa* [Chou & Lu, 1978: fig. 4]), possibly in order to accommodate an extremely long vesica when retracted (Holloway, 1985). A dorso-basal origin of the cuticular simplex appears to have been convergently acquired by *Magusa* and the euteliines.

158 (0·400) Restriction of the aedeagus sclerotization to a ventral band is synapomorphic for the Argyrogrammatini and Plusiini, although there has been a reversal to a uniformly sclerotized aedeagus in *Autoplusia* + *Antoculeora*. Further reduction of the sclerotization to a narrow, well-defined ventral strip is apomorphic for the Argyrogrammatini but has been independently acquired by the autoplusiine genera *Macdunnoughia* and *Erythroplusia*.

159 (0·500) A vesica that is entirely covered with small spines unites *Plusiotricha* and *Eutheiaplusia*, but also occurs in *Thysanoplusia*.

160 (1·000) A strongly serpentine inverted vesica is also synapomorphic for *Eutheiaplusia* and *Plusiotricha*.
161 (1·000) The presence of a small oval sclerotized plate at the base of the ductus ejaculatoris is synapomorphic for the Stictopterinae and Euteliinae.
162 (0·111) The distribution of states of this character was discussed in part above in connection with the positions of *Agrapha* and *Plusiopalpa*. The presence/absence of a subapical cornutus (SAC) is highly homoplasious, with several ambiguous assignments of character states to the internal nodes. Initially, the presence of a SAC is synapomorphic for the Argyrogrammatini + Plusiini. However, there have been numerous independent losses, in clades 7, 30 and 44, and in *Lamprotes* and *Eosphoropteryx*. Loss can also be interpreted as having occurred in clade 12, with subsequent regains in *Agrapha* and *Argyrogramma* + *Stigmoplusia*, but several alternative sequences of change are possible, including independent losses in *Plusiotricha* + *Eutheiaplusia*, *Ctenoplusia* + *Acanthoplusia* and *Plusiopalpa*. Given that *Eutheiaplusia* may have a SAC (see Characters) and many ctenoplusias definitely do (see 648-step cladograms: *Agrapha* and *Plusiopalpa*), multiple independent losses may represent the most likely events.
163 (1·000) An apically swollen SAC is synapomorphic for *Panchrysia* and *Chrysanympha*.
164 (1·000) A SAC arising from a circular concave plate is synapomorphic for *Euchalcia* and *Adeva*.
165 (0·500) A SAC originating on a lateral diverticulum has arisen convergently in *Polychrysia* and *Diachrysia*.
166 (1·000) This character (grooved/'winged' SAC) was discussed above in detail with regard to the branching sequence of *Plusia*, *Cornutiplusia* and *Autographa*.
167 (1·000) The presence of an invaginated sac in the vesica is autapomorphic for clade 6.
168 (1·000) A vesica in which the base is internally granular is autapomorphic for clade 24.
169 (1·000) Only the Abrostolini possess a ventral, apical, blunt point to the vesica sclerotization. This is autapomorphically modified into a hook in *Abrostola*.
170 (1·000) A large membranous RHS diverticulum on the vesica, bearing cornuti is synapomorphic for *Abrostola* and *Mouralia*.
171 (1·000) A dorsal patch of curved cornuti is synapomorphic for the members of clade 26.
172 (0·500) The presence of two, short, straight cornuti on the vesica is apomorphic for clade 7, although there has been reversal in *Chrysodeixis*. In this genus, the position of the short cornuti is occupied by a series of large cornuti. Further studies are required to determine whether these two forms of cornuti are homologous.
173 (1·000) A differentially sclerotized band of RHS sclerotization on the vesica is autapomorphic for the Argyrogrammatini.
174 (1·000) A dorsal convex rounded plate on the vesica is synapomorphic for the members of clade 7.
175 (0·333) Auricular cornuti have been convergently derived in *Eosphoropteryx*, *Loboplusia* and *Macdunnoughia*.

Female abdomen A1–7

176 (0·333) A thickened pleuron on A7 is synapomorphic for the members of clade 31 (with an uncertain loss in *Loboplusia* – see Characters), but with a convergent derivation in *Brachionycha*.
177 (0·500) Concave lateral edges to T7 are also apomorphic for clade 31 (but with a subsequent reversal in *Puriplusia*), and thereby confirm the possible correlation with the previous character.
178 (0·667) A pleural pouch is interpreted as being synapomorphic for the Plusiinae, Stictopterinae and Euteliinae, but with secondary loss in *Magusa*. The latter interpretation is supported by the presence in *Magusa* of a slight pouch, although this is not enlarged as in the three subfamilies. However, this conclusion must, for the present, be treated with caution for an alternative optimization of states interprets the pleural pouch as an independent derivation in the Plusiinae and in the Stictopterinae + Euteliinae. A small, concealed pleural pouch is autapomorphic for the Euchalciina.

Anal papillae and A8–A9+10 intersegmental membrane

179 (1·000) Flared anal papillae are synapomorphic for the Euteliinae and Stictopterinae.
180 (0·500) The Stictopterinae + Euteliinae and *Calophasia* have convergently acquired densely setose inner surfaces to the anal papillae.
181 (1·000) Frayed edges to the anal papillae are autapomorphic for the Stictopterinae.
182 (1·000) A differentiated dorso-ventral row of setae on the anal papillae is an autapomorphy of the Plusiinae.
183 (0·500) Short anal papillae characterize clade 22, but with reversal in *Euchalcia*. Several species of *Euchalcia* (e.g. *E. italica* (Staudinger), *E. dorsiflava* (Standfuss), *E. augusta* (Staudinger)) have even

more modified anal papillae, in which the apices are ventrally produced into acute points (Dufay, 1968). Although the biology of these taxa is unknown (Dufay, 1968), similar modifications in the heliothine genus *Schinia* Hübner are associated with oviposition deep in flowers and unopened buds. Thus state 0 in *Euchalcia variabilis* may merely represent an early stage in a reversal transformation series from short anal papillae to the highly-derived, blade-like forms.

184 (0·500) The presence of an eversible dorsal pouch between the anal papillae and A8 can be interpreted either as autapomorphic for the Plusiinae, with reversal in the Abrostolini, or as independently derived in the Omorphinini and the Argyrogrammatini + Plusiini.

185 (1·000) A sub-basal dorsal flange on the posterior apophysis is autapomorphic for clade 6.

186 (1·000) Thickened membrane between the LPV and the anal papillae is synapomorphic for *Plusidia, Lamprotes* and *Pseudeva*.

A8, ostium bursae & antrum

187 (1·000) A subdorsal, longitudinal, desclerotized band on T8 is autapomorphic for the Abrostolini.

188 (1·000) A ventral pocket on the anterior edge of T8, dorsal to anterior apophysis, is also autapomorphic for the Abrostolini.

189 (0·250) T8 has become irregularly cut back antero-subventrally below the origin of the anterior apophysis independently in *Anagrapha*, clade 44 and clade 30 (but with reversal in *Antoculeora*).

190 (0·500) Anterior apophyses have been independently lost in *Lophoptera* and the euteliines, or lost in the Stictopterinae + Euteliinae and regained in *Stictoptera*.

191 (0·125) 'Protected' ostia bursae, as suspected (see Characters), have been acquired independently no less than eight times, in *Brachionycha, Mouralia, Diachrysia, Rachiplusia, Antoculeora, Lamprotes*, clade 32 and clade 44. When the true homologies of these structures have been determined, more information may be forthcoming but at present this character is useless.

192 (1·000) Spinose pads lateral to the ostium bursae unite *Macdunnoughia* and *Puriplusia*, with the further development into recurved spinose grooves autapomorphic for the latter genus.

193 (1·000) Short, dense, upright scales near the mouth of the antrum are synapomorphic for the members of clade 30.

194 (0·667) As initially suspected, setae along the inner ventral edge of the antrum (state 2) are convergently derived in *Diloba* and clade 26. *Lamprotes* is autapomorphic in that the setae are restricted to a subventral and lateral position (state 1).

195 (0·500) A ventro-anterior extension of T8 shows the same distribution of states as character 190 and thus has the same two alternative sequences of state change.

196 (0·167) An open, shallow antrum has been independently acquired on a total of six occasions, in *Diloba, Cucullia, Chalcopasta, Agrapha, Pseudoplusia* + *Chrysodeixis* and clade 21. A more thorough analysis of the homologies of the states of this character may reduce the homoplasy and allow more reliable information to be extracted from it.

197 (0·500) An entirely membranous antrum has been convergently derived in *Stictoptera* and *Ctenoplusia* + *Acanthoplusia*.

198 (1·000) State 1 of this character, in which the ventral edges of T8 are extended towards the midline, unites the members of clade 35. Further extension (state 2) is synapomorphic for the included genera *Autoplusia* and *Antoculeora*. State 3 (T8, antrum and LPV entirely fused ventrally) arises *de novo* from state 0 in *Rachiplusia*.

199 (1·000) The anterior apophysis arises level with the ventral edge of T8 only in *Autoplusia* and *Antoculeora*.

200 (1·000) A heavily sclerotized, smooth, open antrum is also synapomorphic for *Autoplusia* and *Antoculeora*.

201 (0·200) Thick, white membrane lateral to the ostium bursae has arisen five times independently in *Plusiopalpa, Allagrapha, Lamprotes, Euchalcia* and clade 44.

202 (0·500) This character (T8 represented by a thin band dorsally) has the same distribution and choice of state change sequences as 190 and 195.

Ductus bursae and corpus bursae

203 (0·667) A long, narrow ductus bursae is interpreted as apomorphic for clade 9 but with a reversal in the included clade 14. *Trichoplusia* is autapomorphic for an extremely long ductus bursae (state 2). Given that the females of *Plusiotricha* are currently unknown, and both *Trichoplusia* and *Thysanoplusia* are heterogeneous for states 2 and 1 respectively, very little confidence can be placed in this character at present.

204 (0·500) A corpus bursae that is produced at right angles to the long axis of the ductus bursae shows

the same distribution and heterogeneity of states as the last, and is therefore subject to the same reservations.

205 (0·200) Thickened white membrane on the corpus bursae at the entry point of the ductus bursae has been independently acquired by *Cucullia, Trichoplusia, [Plusiotricha +] Eutheiaplusia* and clade 24 (but with subsequent loss in *Lamprotes* + *Pseudeva*).

206 (0·500) An expanded portion of the ductus bursae with dorsally recurved edges has been convergently derived in *Rachiplusia* and *Macdunnoughia* + *Puriplusia*.

207 (0·500) A short, lateral pouch on the ductus bursae occurs independently in *Agrapha* and *Chrysodeixis*.

208 (1·000) A small corpus bursae with highly elastic walls is synapomorphic for *Diloba* and *Brachionycha*.

209 (0·182) The position of the origin of the ductus seminalis on the corpus bursae is highly homoplasious and highlights the need alluded to above for a critical study of the homologies of the structures variously referred to as the fundus, apex and appendix bursae. The plesiomorphic condition appears to be an apical origin. Independent shifts to a fundular origin have occurred in *Erythroplusia, Puriplusia, Loboplusia, Panchrysia, Oncocnemis, Cucullia* and the Argyrogrammatini. Within the last, reversal has occurred in *Pseudoplusia* and clade 10, with re-reversal in *[Plusiotricha +] Eutheiaplusia*. However, at least two of these homoplasies (*Puriplusia* and *Loboplusia*) may be due to errors in deciding which end of the corpus bursae represents the fundus and which the apex (see also Ichinosé, 1962*b*). For the present, character 209 is best dismissed as unreliable.

210 (0·667) Regular ridges on the corpus bursae have been convergently derived in clade 47 and *Cucullia* + *Calophasia*. Further modification to form a more or less circular pattern unites the Stictopterinae and Euteliinae.

211 (0·667) A concave, circular signum unites the Stictopterinae and Euteliinae but is lost in *Anuga* and further modified into a ridge in *Lophoptera*.

212 (1·000) A distinct differentiation of sclerotization of the corpus bursae granulations is synapomorphic for *Sclerogenia, Autoplusia* and *Antoculeora*.

213 (0·333) State 1 (granular ridges on the corpus bursae apex) is autapomorphic for *Eosphoropteryx*. Sclerotized ridges (state 2) either unite the members of the Autoplusiina, with subsequent loss in *Erythroplusia*, or are convergently derived in *Rachiplusia* and clade 31. Within the latter, very large, strong folds have either arisen in clade 31, only to be lost independently in *Loboplusia* and *Allagrapha*, or have been convergently acquired by clades 33 and 35. Only further examination of additional taxa will resolve these ambiguities but character 213 is undoubtedly important in assessing the interrelationships of the autoplusiine taxa. State 2 has also been convergently derived in *Diloba, Chalcopasta, Omorphina* and *Plusiopalpa*.

214 (0·250) A recurved apex of the corpus bursae has been convergently derived in *Pseudoplusia* and clade 14. However, reversal is interpreted to have occurred in *Acanthoplusia* and *Stigmoplusia*.

215 (0·429) This character was discussed in detail above in connection with the positions of *Plusia, Cornutiplusia* and *Autographa*. State 1 (a patch of thickened membrane on the RHS corpus bursae) is apomorphic for clade 40 but with a reversal in clade 44. State 2 (a shallow pouch) unites *Autographa bractea* and *Cornutiplusia*, while state 3 (a large pouch or appendix) is autapomorphic for the latter genus. State 3 arises *de novo* from state 0 in *Calophasia*.

Miscellaneous

216 (0·500) *Autoplusia* and *Rachiplusia* are interpreted as being convergently sexually dimorphic.

Clade analysis

Each clade, as numbered in Figs 27, 28, is followed by its name (if applicable) and a list of its apomorphies in square brackets. The states printed in italics are those that are considered to be unique and unreversed synapomorphies. For those characters in which the state assignments to the internal nodes are ambiguous, the optimizations described in the preceding section are employed. It should be remembered, however, that these do represent only one of many possible interpretations.

Clade 1: Plusiinae [15(1), 27(1), *29(1)*, *31(1)*, 32(0), 33(0), 35(0), 49(1), 131(1), 143(3), *182(1)*, 184(1)]. The Plusiinae have been conventionally defined as the lashed-eyed, quadrifine noctuids. This study has demonstrated that this characterization is inadequate. Many of the outgroup taxa have lashed eyes (although it must be admitted that several were chosen for inclusion in this investigation expressly because they displayed this state), while one plusiine genus (*Mouralia*) has a distinctly trifine hindwing venation. Detailed study of the condition of hindwing vein M_2 showed that there are various degrees of reduction (see

character 15) and that a straightforward division into present and reduced/absent is too simplistic. Thus, a new characterization of the subfamily must be formulated.

Of the 11 character states listed above, four are unique and unreversed for all members of the Plusiinae and support the monophyly of the subfamily. Thus, the Plusiinae can be defined, on present evidence, as those noctuids with a convex occiput (character 29); few apical styloconic sensilla on the proboscis (31), which has strengthening bars that are semicircular on the most apical portion (35); and anal papillae that bear differentiated, dorso-ventral rows of setae (182).

With the possible exception of the last, however, these characters are not particularly useful as key characters. Several of the other seven homoplasious characters listed above are more suited to this role, providing that the exceptions are recognized and noted. Their inclusion results in a polythetic, but nevertheless workable, definition of the Plusiinae. The other characters are of three types. First, and most important, is character 184, the apomorphic state of which (the presence of an eversible dorsal pouch between the anal papillae and A8) is interpreted as characterizing the Plusiinae. Although it appears to have been lost in the Abrostolini, this pouch has not yet been found in any other group of noctuids and constitutes additional evidence corroborating the monophyly of the Plusiinae. Second, there are those in which the apomorphic state is found in all the plusiines but also occurs in one or more of the outgroup taxa: triangular pilifers (27; also found in *Calophasia*); a long, thin proboscis (32; also found in *Calophasia* + *Cucullia*), with smooth styloconic sensilla (33; also occurring in *Cucullia*); and a large thoracic crest (49; present also in *Chalcopasta*). Third, the apomorphic state may not only occur in the outgroups, but may also be transformed within the Plusiinae into other states, which themselves are found in the outgroups or are homoplasious within the Plusiinae. These are: a hindwing vein M_2 that is half as strong as M_3 (15; this state also occurs in *Diloba*, while within the plusiines, it is transformed into state 2 [a vestigial vein M_2] in *Mouralia*); the presence of saccular flanges (131; these are lost in the Abrostolini, *Trichoplusia* and *Autoplusia*); and a clavus borne on a peninsula on the sacculus (143; this condition is further modified in the Abrostolini and *Anagrapha* into state 2, in which the dorsal and ventral margins of the clavus are basally more or less level, convergent upon the condition found in *Cucullia*).

Thus, it would appear that the key characters commonly used in the past are generally either too homoplasious (have too many exceptions to be of use to the non-specialist) or, on close examination, prove to have been misinterpreted. It is becoming increasingly apparent that satisfactory diagnoses of higher-level taxa will in future rely increasingly heavily upon character states that are not easily observable. This is a price that must be paid for a predictive and useful higher-level classification.

The subfamily Plusiinae is represented throughout the World, with the exception of Antarctica and perhaps some of the more remote oceanic islands. A large number of species occur in Africa and the eastern Palaearctic, while, in comparison, the fauna of South America is relatively depauperate. Plusiines appear to be largely absent from tropical lowland forest habitats, while they reach their greatest diversity in tropical montane and temperate areas. Twelve species occur in Great Britain, either as residents or regular immigrants (e.g. *Autographa gamma*), while rare immigrants (e.g. *Thysanoplusia orichalcea*), singleton occurrences (e.g. *Ctenoplusia accentifera* Lefevbre) and doubtful natives (*Euchalcia variabilis*) account for a further twelve species. They rejoice under such common names as the Spectacle (*Abrostola triplasia*), the Beautiful Golden Y (*Autographa pulchrina* (Haworth)), the Burnished Brass (*Diachrysia chrysitis*) and the Gold Spot (*Plusia festucae*). Elsewhere in the World, the common names of plusiines are less imaginative, if perhaps more practical; for example, le Gamma (*Autographa gamma*), the Bean Leaf Skeletonizer (*Autoplusia egena*) and the Soybean Looper (*Pseudoplusia includens*).

Few generalizations can be made regarding plusiine biology. The adults fly strongly and a number of species are migratory. However, they do not appear to be particularly attracted to light (Warnecke, 1953; Moucha & Novak, 1956; Eichlin & Cunningham, 1978). Thus a light-trap is neither an efficient nor accurate method for assessing plusiine population densities. Eichlin & Cunningham (1978) related an anecdotal observation that although numerous plusiines were observed feeding at night from flowers of a Button Bush (*Cephalanthus occidentalis*) that was growing less than 15 feet from a black light trap, only two moths actually came to the light. Many plusiines fly equally by day and by night. Silver Ys (*Autographa gamma*) are frequently seen in Britain on sunny late summer days feeding from Michaelmas Daisies (*Aster* spp.) in the company of butterflies and bees.

As far as is known, temperate region species are univoltine, while in warmer climates, several generations per year seem likely. However, it should be stressed that only a minority of life histories, particularly of tropical species, has so far been elucidated. Multiple matings appear to be the rule, and the eggs are generally laid singly on the larval foodplant, probably between 200 and 300 per female (Eichlin & Cunningham, 1978). Plusiine larvae are usually green with white, often interrupted, longitudinal stripes. The head may bear a black, lateral stripe. Several species are sensitive to population density, becoming darker when overcrowded (Ichinosé, 1959). There are generally five larval instars but a few species pass

through six or even seven. In most species, the prolegs on segments A3 and A4 are reduced or missing (see below) and the larvae proceed by a looping action, thus giving rise to their common name of semiloopers. Pupation is usually in a cocoon spun between leaves. Pupal coloration has been shown to be temperature dependent in at least one species (Ichinosé & Asawa, 1964) with darker pupae being formed at lower temperatures. According to Eichlin & Cunningham (1978), the prepupal stage lasts 1–2 days and the adults emerge about eight days after pupation. Little is known about plusiine courtship behaviour, but judging from the widespread occurrence of various tufts, brushes and pouches, pheromones produced by both sexes are likely to play an important role (see Gothilf & Shorey, 1976, for a comprehensive account of courtship in *Trichoplusia ni*).

Omorphinini [7(1), 20(0), 24(1), 42(1), *52(1)*, 59(1), 127(1), 137(1), 144(1), 147(1), 213(2)]. This tribe consists of a single genus and species, *Omorphina aurantiaca*. Of the character states listed above, ten are homoplasies occurring elsewhere in the Plusiinae or among the outgroups. This is only to be expected since the genus-level autapomorphies were largely eliminated from the data set prior to the analysis. However, characters 7 (yellow hindwings), 20 (randomly arranged scale bases), 24 (a prominent rim around the eye) and 137/147 in combination (oval valves with setae arising from marginal prominences) are useful recognition features. In addition, state 52(1), a truncate dorsal tegular arm, is autapomorphic. Although considered by Kostrowicki (1961) to be more correctly treated as an acontiine, the presence in *Omorphina* of the character states listed above for clade 1 argue strongly that Hampson (1913) was correct in placing the genus in the Plusiinae.

Omorphina aurantiaca (Fig. 31) is a small moth, recorded only from Xizang Province, China (Tibet) and Sikkim, at around 15,000 ft (4500 m). Nothing is known about its biology except that the adult flies in July (Alphéraky, 1892). *Omorphina* has previously been likened to the Palaearctic amphipyrine *Panemeria tenebrata* (Scopoli) (Alphéraky, 1892), but apart from the presence of marginal prominences on the valves, the genitalia of the two genera are dissimilar in both sexes. In particular, *Panemeria* lacks the row of setae on the anal papillae, while the cornuti on the vesica are very similar to those of *Chalcopasta*, which may indicate that the true affinities of *Panemeria* may lie with the Stiriini.

Clade 2 [10(1), *28(0)*, 58(1), *73(1)*, *80(1)*, *99(1)*]. This clade, which comprises all the Plusiinae except *Omorphina* (Omorphinini), is well supported by four unique and unreversed apomorphies: a dorsally delimited frons (28); an internal flange on the anterior edge of T2 that is produced subdorsally (73; see also clade 4); a particular form of St8 and ventral hair pencil (80), although this is frequently further modified; and the presence of a notch between the tegumen and uncus (99). In addition, all members of clade 2 display a metallic sheen over much of the forewings, although this is often weak and difficult to observe (10; the condition in *Chalcopasta* is almost certainly convergent but needs to be checked in other members of the Stiriini), and often bear a white spot on the fore tibia (58; this is frequently lost in the Plusiinae, occurs also in *Chalcopasta* and the Euteliinae, and is often impossible to score in many taxa due to additional pattern modifications).

Clade 3: Abrostolini [1(1), *2(1)*, *51(1)*, *100(1)*, *102(1)*, *103(1)*, 107(1), *124(1)*, *125(1)*, *126(1)*, 131(0), *134(1)*, 143(2), *169(1)*, *170(1)*, 184(0), *187(1)*, *188(1)*]. There can be no doubt that the abrostoline genera *Abrostola* and *Mouralia* form a monophyletic group. Of the 18 character states listed above, no fewer than 13 are unique and unreversed. Members of the tribe are best recognized by the form of the forewing stigmata (2), the fusion of the aedeagus to the juxta apex (124), the spatulate saccular lobe (134) and the desclerotized band and invaginated pocket laterally on T8 in the females (187/188 respectively). In addition, they are the only plusiines to possess raised scales in the forewing cell (1) and to lack an eversible pouch between the anal papillae and A8 in the females (184). Uniquely in the subfamily, as far as is known, the larvae of the Abrostolini bear prolegs, albeit somewhat reduced, on abdominal segments 3 and 4 (Eichlin & Cunningham, 1978; see also below), although this condition is probably plesiomorphic.

Abrostola [22(2), 121(2), 143(1), 169(2)]. This genus is probably paraphyletic relative to its sister-taxon *Mouralia*. The ventral hook on the vesica (169) and the heavily lashed eyes (22) appear to be restricted to *A. triplasia* (Fig. 32) and a few other, possibly closely related, species (e.g. *A. kaszabi* Dufay [Dufay, 1971]; *A. trigemina* (Werneberg)). The blunt, lobate VAVB (121) and the broad, rounded clavus (143) need to be confirmed in the other species of *Abrostola*.

Abrostola includes about 35 species, of which four are North American and the remainder almost equally divided between Africa and the Palaearctic. None are known from South America, South East Asia or Australasia. Many species have only recently been described, particularly important contributions in this respect being those of Dufay (1957; 1958; 1960; 1971). The larvae of *Abrostola* are characteristic in

having a 'humped' segment A8, usually bearing two small, subdorsal points. In most species (e.g. *A. triplasia, A. trigemina, A. major* Dufay), there are diagonal, subdorsal white or cream stripes on segments A1–8, together with darker, more dorsal markings. On segments A1, A2 and A8, the latter fuse to form single, dorsal spots, which, together with the more pronounced pale markings, produce a very distinctive, somewhat eye-like, pattern. The overall colour can vary from green to violet-brown. The larva of *A. asclepiadis* is very different. A single, dried, inflated skin in the BMNH collection is uniform pale cream (?green in life), and is covered in a pattern of small, black spots, not all of which are associated with setal pinacula. The pattern is suggestive of an aposematic colour scheme, which is not unreasonable given the species' asclepiadaceous foodplant (see below). However, this hypothesis remains to be corroborated by the description or a colour photograph of a living larva. The biology of only a few species is known, primarily from the Holarctic fauna. Most species for which the larval hostplant is known feed on Urticaceae; usually *Urtica* itself (Crumb, 1956; Beck, 1960; Ichinosé, 1962b; Bretherton *et al.*, 1983; Miyata, 1983), but *A. anophioides* Moore utilizes *Girardinia heterophylla* (Gardner, 1947), while *A. trigemina* and *A. major* also feed on *Boehmeria*. *A. abrostolina* (Butler) is recorded from *Fatoua* (Moraceae) (Miyata, 1983), and other recorded foodplants include *Epilobium, Lamium* (Hampson, 1913) and *Humulus* (Bretherton *et al.*, 1983). One species is exceptional, however, in that it has performed a remarkable hostplant shift; *A. asclepiadis* is the only plusiine known to feed exclusively on an asclepiad, *Vincetoxicum hirundinaria* (Hampson, 1913 as *Cynanchum vincetoxicum*; Beck, 1960; Weidlich, 1984 as *Vincetoxicum officinale*). Members of *Abrostola* are also unusual among the plusiines for overwintering in the pupal stage rather than as early instar larvae (Eichlin & Cunningham, 1978). The British species are known as 'spectacles' from the markings on the patagia, but this pattern is not found throughout the genus.

Mouralia [14(2), 15(2), 18(2), 19(1), *64(3), 83(5), 136(1),* 191(1)]. *Mouralia* currently includes only a single described species, *M. tinctoides* (Fig. 33). Of the above eight listed character states, three constitute good autapomorphies for the genus: the presence of spines on the *inner* surface of the hind tibia (64); the extremely long sternal hair pencil, arising from a single pocket that almost reaches the base of the abdomen when retracted (83); and the presence of basally-directed scales on the valve apex (136). Although this latter condition was coded as also present in the Argyrogrammatini (q.v.), the form of the scales differs and so the two conditions probably represent distinct characters. In the Argyrogrammatini, the scales are simple and setose, often quite stiff and usually easily detached, while in *Mouralia*. these scales are long, soft, curved, apically spatulate and persistent (Fig. 348). In addition, *Mouralia* is the only plusiine with a trifine hindwing venation (15) and has a female frenulum reduced to two setae (14; a condition also found in clade 6, *Rachiplusia, Autoplusia* and *Brachionycha*).

There are also numerous abdominal and genitalic autapomorphies that were not included in the analysis. These include: a long, thin, medial apodeme projecting anteriorly from the anterior margin of St7 in the male (this may be functionally correlated with the long hair pencil pocket); an apically, laterally flattened uncus (Fig. 278); a pair of spatulate flaps arising from the dorsal sclerotized band on the anal tube; an ampulla (Fig. 348); valves thickly covered ventrally and exteriorly with long, flexuous, pale yellow, 'sticky' (in the sense that they adhere to forceps) scales; valves in which the apices turn through 90 degrees so that the costal edges become internal and the saccular edges become external (Fig. 348); and a corpus bursae with a very elongate, tapering fundus that broadens to a blunt tip.

A second undescribed species of *Mouralia* has recently been discovered in Bolivia (F. Navarro, pers. comm.). It differs in several features from *M. tinctoides*. The most notable of these are (as assessed from a photographic slide of a male genitalic preparation) the presence of only a rudimentary hair pencil and a valve apex that lacks all the modifications of *M. tinctoides*, simply tapering to a point as in many abrostolas. Thus this new species may represent an intermediate form between the genus *Abrostola* and *Mouralia tinctoides*.

Another candidate for such an intermediate taxon is *Abrostola anophioides*. This is a large species found in the Himalayan foothills from Uttar Pradesh in NW. India to Sichuan Province, China. Unlike other abrostolas, the males of *A. anophioides* have a short, single hair pencil, while the fundus of the corpus bursae is elongate and apically swollen as in *Mouralia tinctoides*. *A. anophioides* and the new *Mouralia* species strongly suggest that one result of a detailed study of the Abrostolini might be the synonymy of *Mouralia* with *Abrostola*.

Mouralia tinctoides is widespread throughout the Neotropics, penetrating as far north as the SW. United States. Its life history has been described in detail by Comstock (1937). The general appearance of the larva is that of an *Abrostola* but it differs markedly in hostplant, feeding on *Tradescantia fluminensis* and *Zebrina pendula* (Commelinaceae) (Eichlin & Cunningham, 1978) (although the latter may be an error; Eichlin, 1975). Unusually for the Plusiinae, there are seven larval instars (the norm is five).

Clade 4 [3(1), 4(1), 6(1), 59(1), *73(2)*, 83(3), 106(1), *157(2)*, 158(1), 162(1)]. The Argyrogrammatini and the Plusiini are united as sister-groups primarily on the basis of two synapomorphies: a distinct, bulbous coecum (157) and a unique form of the internal flange on the anterior edge of T2, in which the two subdorsal lobes (see clade 2) are fused medially but with a medial ventral emargination (73). In addition, several character states occur only in clade 4, although in not all of the constituent genera; these are the characteristic plusiine Y-mark (3), a pink terminal line on the forewing (4, see also clade 25), a scale tooth (6), restricted sclerotization on the aedeagus (158) and a subapical cornutus (162). Further, in all members of the Argyrogrammatini and Plusiini, the LASTs are fused around the base of the uncus, although this condition recurs in *Chalcopasta*.

As far as is known, all members of clade 4 that hibernate do so as early instar larvae. Also, the prolegs are vestigial or absent on segments A3 and A4 in all larval instars (but see *Anadevidia*).

Clade 5: Argyrogrammatini [14(1), 18(0), *89(1)*, 108(1), *136(1)*, 144(1), 158(2), *173(1)*, 209(1)]. This primarily tropical tribe of plusiines is quite well characterized by three synapomorphies. All argyrogrammatines have secondary hair brushes arising on St8 (89), basally-directed setose scales apically on the valve (136, see also *Mouralia*), and a differentially sclerotized band on the vesica (173). Seta 1 of the female frenulum is also reduced (14; see *Mouralia, Autoplusia, Rachiplusia*) and the ventral sclerotization of the aedeagus is further restricted to a distinct narrow band (158; with convergence occurring in the autoplusiine genera *Erythroplusia* and *Macdunnoughia*).

Anadevidia [3(0), 6(1), 105(1), 116(1), 148(0)]. *Anadevidia* is an enigmatic genus, of somewhat uncertain position. Both Kostrowicki (1961) and Ichinosé (1962*b*) refrained from making any explicit statements as to its relationships, although the latter derived the larval setal pattern from that of *Thysanoplusia* (as *Diachrysia*), a relationship formalized by Chou & Lu (1979) as the 'Plusiini'. Kljutshko (1985*b*) placed *Anadevidia* in the Plusiini, where it remained after the reanalysis performed above, on the basis of lack of prolegs in the mature larva and setae SD1 on segment A9 being 'normal'. This similarity to members of the Plusiini is supported further by character 116, in that both taxa possess a strongly concave pleurite. However, as described above, there is stronger evidence (characters 89, 136 and 173) to suggest that *Anadevidia* correctly belongs in the Argyrogrammatini.

It may yet be shown that *Anadevidia* is in some way related to *Chrysodeixis* (+ *Pseudoplusia*). Both genera bear spatulate scales on segment A8 in the male (although these are interpreted here as independent conditions). Also, the vincular arms in *Anadevidia* are long and narrow, and superficially resemble those of *Chrysodeixis* and *Pseudoplusia*, although they are separate in the former genus and intimately fused into a thin spine in the latter two.

Anadevidia currently contains only two species, *A. peponis* (Fig. 34) and *A. hebetata*. The former is widespread throughout the Indo-Australian region, while the latter is apparently restricted to India and Japan. In general appearance, they are dull grey-brown moths with no distinguishing pattern features, and bear a superficial resemblance to species of the genera *Allagrapha* and *Diachrysia* (especially *D. leonina* and *D. bieti* (Oberthür)). The larvae of *Anadevidia* have several unusual features. They are the only plusiines in which the first instar larvae possess on segments A3 and A4 well developed prolegs that are subsequently lost completely in the later instars. The larvae also bear enlarged pinacula on some segments, giving them a warty appearance. *Anadevidia* is oligophagous, feeding on members of the Cucurbitaceae, although *A. peponis* has been recorded from *Mercurialis* (Euphorbiaceae) and *Paulownia* (Scrophulariaceae) (Miyata, 1983). The larval chaetotaxy of *Anadevidia* has been described by Ichinosé (1958*b*; 1962*a*; *b*).

Clade 6 [12(1), 14(2), *76(1)*, 77(1), 83(2), 91(1), 94(2), 110(1), *167(1), 185(1)*]. Three very good synapomorphies characterize clade 6: the form of St7 in the male (76); the presence of an invaginated sac in the vesica (167); and the presence of a sub-basal dorsal flange on the posterior apophysis (185). The males of the majority of the constituent taxa also bear dorso-lateral hair tufts on at least segments A5 and A6 (77, except *Zonoplusia* and *Pseudoplusia*), have dorsally twisted lateral arms of St8 (91, except *Pseudoplusia*) and have broad, 'greasy' scales apically on the dorsal arms of St8 (94, again, except *Pseudoplusia*). Overall, clade 6 is very well supported, allowing for the multiple reversals of *Pseudoplusia* (q.v.).

Clade 7 [93(1), 105(1), 108(0), 128(1), 162(0), 172(1), *174(1)*]. The three genera of this clade are united by a single synapomorphy, a dorsal, convex, rounded plate on the vesica basally (174). In addition, a pair of short, straight cornuti occur in both *Dactyloplusia* and *Pseudoplusia*, but not in *Chrysodeixis* (172). However, as discussed above (Character analysis), the condition in the latter genus may prove to be derivable from that in the former two. Also, all three genera have a juxta that is apically scobinate (128), although this condition recurs in *Thysanoplusia, Plusiopalpa* and *Cucullia*.

Dactyloplusia [60(1), *78(1)*, 80(2), 92(1), 110(0), 149(1)]. In the present analysis, *Dactyloplusia* is interpreted as being the sister-group of *Chrysodeixis* + *Pseudoplusia*, on the basis of the characters listed above for clade 7. However, there are an almost equal number of character states that suggest *Dactyloplusia* may instead be related to clade 10, and in particular, *Thysanoplusia*. These include the presence of a hind basitarsal comb (60), latero-ventral flaps on the anterior bar of St8 (80), a sub-basal lobe on the lateral arms of St8 (92), a sharply hooked harpe (149), as well as the apically scobinate juxta referred to in the preceding paragraph. *Dactyloplusia* is also autapomorphic in having the dorso-lateral hair tufts on segment 7 enclosed in a groove (78).

Dactyloplusia currently contains only a single species, *D. impulsa* (Fig. 50). Holloway (1985) gives the distribution as Sri Lanka, India, S. China, Sundaland, Sulawesi and New Guinea. However, by far the majority of specimens in the BMNH collection were caught in Sri Lanka. Nothing is known of the biology of *D. impulsa*. Holloway (1985) captured a Bornean specimen 'on a river bank with disturbed vegetation and alluvial forest near a limestone cliff at 100 m'.

Clade 8 [11(1), *111(1)*, *120(1)*, 130(0), 144(0), 196(1)]. A sister-group relationship between *Pseudoplusia* and *Chrysodeixis* is hypothesised on the basis of two synapomorphies: a long, thin, spine-like vinculum (111; the condition found in *Stigmoplusia* is considered to be non-homologous) and a very narrow, almost straight pleurite (120). Ichinosé (1973) also recognized the great similarity between these two genera and thought that *Pseudoplusia* might eventually prove to be best placed in *Chrysodeixis*, perhaps as a subgenus.

Pseudoplusia [59(0), 77(0), 83(0), 91(0), 93(0), 94(0), *128(2)*, 209(0), 214(1)]. *Pseudoplusia* is perhaps most notable for the total reduction of the male scent organs, both those of St8 and the dorso-lateral hair tufts (characters 77, 83, 91, 93, 94). This may prove to be due to the geographic isolation (one species in the Americas, the other on Saint Helena) from other members of clade 7, resulting in a relaxation of the selective pressures that maintained the elaborate scent organs, which were thus lost. *Pseudoplusia* also displays a number of autapomorphies. The males possess a hook-like process near the base of the valve costa, an extremely long, thin, sinuous harpe, and bear a sharp spine medially on the posterior margin of the juxta (Fig. 341; similar to the type of spine found in some species of *Syngrapha*). The juxta is also latero-apically spinose (128). In the females, the apex of the corpus bursae is extremely elongate and tapered, projecting first anteriorly and then recurving posteriorly.

The genus *Pseudoplusia* contains two species, *P. includens* (Fig. 38) and *P. dalei* (Wollaston) **comb. n.** (see Appendix 4). The former is widespread from Canada to Argentina and Chile (Forbes, 1954; Angulo & Weigart, 1975) and is an important pest of many cultivated plants (Canerday & Arant, 1967). It is commonly known as the Soybean Looper (Eichlin & Cunningham, 1978) or, less frequently, the False Cabbage Looper (Canerday & Arant, 1967). An icosahedral virus has recently been isolated from *P. includens* (Chao, Young & Kim, 1984) and may prove useful as a biological control agent. *P. dalei* is endemic to the mid-Atlantic island of Saint Helena. Little is known of its biology except that the adults have been seen frequenting the flowers of geraniums and *Pittosporum* and that it may belong to the nearly-extinct scrubland fauna of the island (Wollaston, 1879).

Chrysodeixis [12(0), *77(3)*, *83(5)*, *94(1)*, 97(1), 105(0), 127(1), 172(0), 207(1)]. In contrast to its sister-genus, *Chrysodeixis* is most notable for the often extreme elaboration of the scent organs on the male abdomen. The progressive reduction of the sternal hair pencils, with the concomitant modification of the secondary hair brushes, T8 and St8, has already been described above (Terminology). In addition, the more derived species, such as *C. chalcites* (Fig. 39), have distinct additional dorso-lateral hair tufts on segment A4 (77); broad, spatulate scales apically on the dorsal arms of St8 (94); and an additional two pairs of hair pencils arising subventrally from discrete pockets in the membrane between segments 7 and 8. In the more plesiomorphic species, *C. argentifera* (Fig. 40), the sternal hair pencils are more fully developed but arise from a single pocket (83), much as in *Mouralia*.

Chrysodeixis is a moderate-sized genus of about 25 species found throughout the Old World tropics. However, by far the majority of species occur in SE. Asia and Australasia. Most are relatively restricted in range but three, presumably by virtue of a strong migratory habit, have become very widespread. *C. acuta* is found more or less throughout the entire range of the genus (Dufay, 1970*a*; Pinhey, 1975). It has even been recorded from Great Britain despite apparently never having been captured on mainland Europe (Bretherton *et al.*, 1983). *C. chalcites* is sympatric with *C. acuta* over the western part of the latter's range, but is replaced by *C. eriosoma* from approximately Indonesia eastwards. There is some debate as to whether *C. chalcites* and *C. eriosoma* are (Pinhey, 1975) or are not (Kostrowicki, 1961; Dufay, 1970*a*) conspecific. The biology of the two species is very similar and although allopatric *C. eriosoma* can be distinguished from *C. chalcites* by differences in the cornuti (Kostrowicki, 1961), in the area where the two

species are thought to overlap, the distinction is not as clear cut and there is confusion as to their identities (Holloway, 1985). *C. chalcites* has also been taken in Great Britain and, in contrast to *C. acuta*, is frequently recorded from Mediterranean Europe (Bretherton *et al.*, 1983).

One section of *Chrysodeixis*, the *minutus* Dufay species-group (Holloway, 1985), does not show the needle-like vinculum but does possess additional hair pencils between segments A7 and A8. The relationships of these species need to be assessed carefully in any future analysis of the interrelationships of the members of clade 8.

Clade 9 [59(0), 203(1), 204(1)]. This clade is not supported by any good synapomorphies and will probably not be corroborated by future studies. Two of the character states, an elongate ductus bursae (203) and a transversely orientated corpus bursae (204), only occur in the included genera *Zonoplusia, Thysanoplusia, Trichoplusia* and *Eutheiaplusia* (with *Plusiotricha* unknown), with both states being subsequently lost in clade 14. However, the apomorphic states for 203 and 204 are not found throughout *Trichoplusia* and *Thysanoplusia* (Dufay, 1970*a*) (*Zonoplusia* and *Eutheiaplusia* are treated here as monotypic) and it is thus highly unlikely that they will be shown in future to support a monophyletic group of genera comprising clade 9 less clade 14. Certainly, before such a study can be attempted, a critical reappraisal of *Trichoplusia* and *Thysanoplusia* must be undertaken (see also *Plusiotricha*).

Zonoplusia [4(0), 58(0), 77(0)]. *Zonoplusia* is treated here as a monotypic genus, comprising only the type species, *Z. ochreata*. When originally erected (Chou & Lu, 1978*a*), five species were placed in *Zonoplusia*. Two were unavailable for examination (*Z. longisigna* (Chou & Lu) and *Z. brevistriata* (Chou & Lu)) but are probably closely related to, if not synonymous with, either of the other two species. These are *albostriata*, a current member of *Ctenoplusia* (for the moment, see 60 and 133) and *daubei*, presently placed in *Thysanoplusia*. Ichinosé (1973) included *Z. ochreata* in *Thysanoplusia*, although it differed from *T. intermixta* and *T. daubei* in the larvae having very fine cuticular ornamentation (like *Chrysodeixis, Trichoplusia* and *Ctenoplusia* s.l.) rather than large and hair-like microtrichia.

Z. ochreata (Fig. 49) is a small moth, in which the Y-mark has been modified into an oblique, pale grey, double line. The subapical cornutus is unusual in that it arises from a sclerotized base that is almost as long as the cornutus, thus giving the appearance of a double cornutus. *Z. ochreata* is found in the eastern Palaearctic and throughout the Oriental tropics and has also been recorded from Queensland, Australia (although otherwise not east of Sundaland and the Philippines (Kostrowicki, 1961; Holloway, 1985)). The only known larval foodplant is *Polygonum thunbergii* (Polygonaceae) (Miyata, 1983).

Clade 10 [80(2), 84(1), 92(1), 93(2), 209(0)]. This clade is also not supported by any good synapomorphies. As was discussed above, states 80(2) and 92(1) are shared with *Dactyloplusia*, which may have its true affinities with members of clade 10. Sclerotized bars on the sternal hair pencil pockets (84) are restricted to members of this clade but are absent in *Thysanoplusia, Plusiopalpa* and *Acanthoplusia*. Similarly, dorsal arms of St8 that are apically fused into a rounded point (93:2) are found only in clade 10, although this state is further modified in clade 18 (93:3) and *Thysanoplusia* (93:1, convergent upon the condition found in *Chrysodeixis* and *Dactyloplusia*).

Clade 11: *Trichoplusia* s.l. [60(1), 83(3), 144(0)]. No unique and unreversed synapomorphies have been found to link *Trichoplusia* and *Thysanoplusia* as sister-groups. The form of the hind basitarsal comb (60), sternal hair pencils (83) and clavus (144) are all probably the plesiomorphic conditions for these characters in the Plusiinae (whether by primary symplesiomorphy or by secondary reversal).

***Trichoplusia* s.str.** [105(1), 110(0), 131(0), 149(1), *203(2)*, 205(1)]. *Trichoplusia* s.str. (i.e. sensu McDunnough, 1944; Ichinosé, 1973) is an extremely heterogeneous genus and appears to have been adopted as the 'dustbin' of the Argyrogrammatini, in much the same way as 'Plusia' s.l. accommodates any generally unplaceable plusiine. As a result, the genus currently contains about 50 species. The remarks made below thus properly refer only to *T. ni*.

The only good autapomorphy for *T. ni* (Fig. 43) discovered in this study was the extremely long ductus bursae (203), which was the main character state emphasised by McDunnough (1944) when he originally proposed the genus. A similar long ductus bursae also occurs, however, in *T. oxygramma* (McDunnough, 1944; Eichlin & Cunningham, 1978) and in *T. gorilla* (Holland) (Dufay, 1970*a*), where it is even longer, being some 3–4 times the length of the body. *T. ni* is the only argyrogrammatine examined to lack a saccular flange (131) and, like *Dactyloplusia* and *Agrapha*, possesses a sharp, hooked harpe (149).

Trichoplusia is badly in need of a critical and thorough revision. Species have been added somewhat casually since Dufay (1970*a*) began the rapid expansion of the genus. It is almost certainly polyphyletic with

regard to at least *Thysanoplusia, Dactyloplusia, Zonoplusia* and *Ctenoplusia*. This much is immediately obvious from the length of the couplet (24 lines) necessary to distinguish *Trichoplusia* from *Ctenoplusia* in Dufay's (1970*a*) key. A flavour for the problem can be gained from the description in the key of the form of the cornuti in *Trichoplusia* (translated freely): 'aedeagus often armed with a small, spiniform or needle-like cornutus, accompanied or not by a mass of fine spicules, or furnished with a large number of spines, or only with a more or less dense edging of denticles; rarely almost unadorned'. The corresponding 'condition' in *Ctenoplusia* reads: 'aedeagus armed with many cornuti or with a large and long, stick-like cornutus, never with a single, fine, spiniform cornutus, sometimes with several small cornuti'. *Trichoplusia* almost certainly contains a number of monophyletic units and their elucidation is probably the most pressing, yet most difficult, task in plusiine systematics.

T. ni is the world's most widespread plusiine. As race *brassicae* (Riley), it occurs from Canada to Central, and even South, America (Kostrowicki, 1961; Eichlin & Cunningham, 1978) and had been introduced into Hawaii by 1939 (Zimmerman, 1958). As race *ni*, the species occurs throughout the southern Palaearctic, Africa and most of the Oriental and Australasian regions, reaching South Africa, Madagascar, Korea and New Zealand. The two races are very dubiously distinct (the forewings of *ni* are said to be lighter and often greyer than those of *brassicae*) and the separation is often not made (e.g. Eichlin & Cunningham, 1978; Franclemont & Todd, 1983).

Commonly referred to as the Cabbage Looper or the Ni Moth, *T. ni* is a very important pest of numerous crop plants, but particularly of brassicas (as one of the common names implies). The list of its larval foodplants is impressive. Eichlin & Cunningham (1978) list over 60 genera from a wide range of families and the species would appear to be able to eat virtually anything, including plants with apparently considerable chemical defences (e.g. *Asclepias, Crotalaria, Euphorbia* and *Senecio*). I reared large numbers, from New Zealand stock, in the BMNH and the only plant that was actively *refused* was the introduced Japanese knotweed, *Reynoutria japonica*. Because of its pest status, *T. ni* has been the subject of much research activity aimed at its control or destruction and this in turn has generated an enormous amount of literature on the subject (see any appropriate abstracting journal).

Thysanoplusia [2(0), 9(1), 84(0), 93(1), 112(1), 128(1), 159(1)]. *Thysanoplusia* was originally erected by Ichinosé (1973) to accommodate those species previously incorrectly placed in *Diachrysia*, due to confusion over type species (see Review). The genus originally included *T. intermixta* (Fig. 47), *T. orichalcea, T. daubei* (Fig. 48) and *T.* (now *Zonoplusia*) *ochreata*. Suggested future candidates for inclusion were *florina, homoia* (Dufay), *ignicollis* (Dufay), *semirosea* (Walker) and *viettei*. Although stated to be separable on the basis of larval and adult characters, the latter were never clearly stated. Thus, the characterization of *Thysanoplusia* came to depend upon larval features. Most notably, *Thysanoplusia* differed in having a very slender seta SD1 on segment A9 and in bearing setae SV1 and SV2 on A2 on a single pinaculum (Ichinosé, 1962*b*; 1973). The genus was retained, with reservations, by Holloway (1985), who added *T. ekekei* (Bethune-Baker) and *T. bipartita* (Snellen). However, most authors treated *Thysanoplusia* as synonymous with *Trichoplusia* (e.g. Dufay, 1975; 1982*b*) and eventually it was so treated in the Japanese checklist (Inoue *et al.*, 1982). Although I accept that *Thysanoplusia* defined in terms of the two larval characters may prove to be a monophyletic unit, until such time as good adult synapomorphies are found (or, alternatively, and far less likely, the larvae of the outstanding species are described), the concept is of limited value. *Thysanoplusia* is best either sunk completely into *Trichoplusia* until a comprehensive revision can be undertaken, or restricted to a group of species centred upon *T. intermixta* (perhaps including *T. daubei* and its relatives), but always remembering that this is at best an incomplete group.

T. intermixta is a member of that subsection of *Thysanoplusia* with a conspicuous metallic golden-green patch on the forewing (9). Five species are currently recognized in this species-group: *T. ekekei* from New Guinea; *T. bipartita* from Sulawesi and Borneo (both these species have diffuse patches); *T. intermixta* from the Oriental tropics as far as Java and Japan (Holloway, 1985); *T. florina*, a Madagascan endemic; and *T. orichalcea*, which is widespread in the Old World tropics and subtropics. Like other highly successful and widespread plusiines (*Trichoplusia ni, Chrysodeixis acuta, C. chalcites, Pseudoplusia includens, Autographa gamma*), *Thysanoplusia orichalcea* is strongly migratory. It is occasionally taken in Great Britain and Scandinavia and has recently become established in New Zealand (1984), possibly from New Caledonia or Australia. Again, like the other successful species, *T. orichalcea* is a serious agricultural pest throughout much of its range, including New Zealand (J. Dugdale, pers. comm.), where it attained this status within a mere 12 months of its recorded arrival.

Clade 12 [12(0), 77(2), 91(2), 138(1), 162(0)]. This clade is another in the Argyrogrammatini that is not corroborated by any good synapomorphies. Two features are restricted to members of this clade: the

presence of weak dorso-lateral hair tufts on segments (A2–)A4 in the male (77) and lateral arms of St8 that are twisted dorsally with a deep, basal concavity (91). However, both of these states are later lost, in clade 16 and *Plusiopalpa* respectively.

Clade 13 [108(0), *140(1)*, 159(1), *160(1)*, 205(1), 209(1)]. *Eutheiaplusia* and *Plusiotricha* are considered to form a sister-group pair on the basis of two character states: a broad, blunt point on the sacculus (140) and the characteristic serpentine form of the inverted vesica (160). In addition, the ornamentation of the vesica is unusual in comprising more or less uniformly distributed small spines (159), a condition that is elsewhere only found in *Thysanoplusia*.

Plusiotricha [11(1), 60(2), 61(1), *112(3)*, 119(1), 133(1), 144(2)]. As discussed above, *Plusiotricha* shares with *Ctenoplusia* and *Acanthoplusia* the unique blade-like setae along the sacculus. In addition, *Plusiotricha* also shares another state with clade 16, a pleurite and VAVB fused for about half the length of the former (119), and has a similar form of basitarsal comb (60) to *Ctenoplusia*. These character states argue strongly that a future, more thorough study may show these three genera (and *Eutheiaplusia*, see below) form a monophyletic unit. *Plusiotricha* is unique in having hook-like projections on the vinculum arms towards their apices (112).

Of more immediately importance would be the discovery and examination of a female of *Plusiotricha*. The genus currently contains three species, *P. livida, P. carcassoni* Dufay and *P. fletcheri* Dufay, represented in collections by seven, one and ten males respectively. A further four males are known that may represent a fourth species (Fig. 51). Female specimens are urgently needed to check whether the predicted female character states, particularly the elongate ductus bursae (203), found in *Eutheiaplusia* do also occur in *Plusiotricha*.

Nothing is known about the biology of *Plusiotricha*. The holotype of *Plusia dyscapna* Fletcher (a synonym of *Plusiotricha livida*) includes a pupal exuvium and final instar larval skin, but no life history information accompanies the specimen. Neither was any mention made of the immature stage material in the original description (Fletcher, 1963). The genus *Plusiotricha* appears to live in mountainous areas at an altitude of about 4000–5000 ft (1200–1500 m) in the tropical rainforest belt of Africa, from the Ivory Coast to Kenya and Zimbabwe (Dufay, 1972). The largest number of specimens has been taken in Tanzania.

Eutheiaplusia [4(0), 83(0)]. *Eutheiaplusia* can be characterized as a *Plusiotricha* in which the male scent organs have become highly reduced and presumably non-functional (83; and thus sits in relation to *Plusiotricha* as *Pseudoplusia* does to *Chrysodeixis*), and in which the blade-like saccular setae are replaced by fine, somewhat flattened, upcurved hairs and the vincular hooks are lacking. It could thus represent either the sister-group of *Plusiotricha* or may eventually prove to be the most basal lineage of a clade comprising the present clades 13 and 16. The vesica of the male illustrated by Dufay (1970*a*) bears a long, thin, subapical cornutus absent in the specimen examined in this study. The presence or absence of this structure in *E. pratti* (Fig. 52) requires confirmation.

Eutheiaplusia comprises a single species, *E. pratti*, endemic to Madagascar. Nothing is known of its biology, although the species appears to be quite widespread on the island in forest at altitudes of between 730 and 1700 m (Dufay, 1970*a*).

Clade 14 [86(1), 87(1), 112(1), 203(0), 204(0), 214(1)]. As was found for clades 9, 10 and 12, there are no good synapomorphies for clade 14. Accessory pouches in the sternal hair pencil pockets (86) occur only in this clade (but not in *Ctenoplusia* or *Plusiopalpa*), as do sternal hair pencils in which the outer scales are shorter than the inner (87; but not in the included clade 17). Dorsal emarginations of the vincular arms (112) do characterize the members of this clade but have been convergently acquired by *Thysanoplusia*.

Agrapha [6(1), 12(1), *79(1)*, 88(1), 98(1), 105(1), 130(0), 144(2), 149(1), 162(1), 196(1), 207(1)]. *Agrapha* currently contains three described species: *A. ahenea, A. meretricia* (Schaus) **comb. n.** and *A. calceolaris* (Walker) **comb. n.** There are also two undescribed species that were allocated manuscript names by E. L. Todd (note in BMNH collection, 1972). One, here termed species A, is represented in the BMNH collection by seven specimens from Colombia, Bolivia and Peru, and includes noctuid genitalia preparation 5193 (male). The second species (sp. B) is unrepresented in the BMNH collection, is of unknown provenance and depository, and was not examined.

Of the included species, three (*A. ahenea* (Fig. 57), *A. meretricia* and sp. A) present a distinctive facies, particularly with regard to the highly developed dorso-lateral hair tufts, which give the abdomen a truncate, bushy appearance. The same three species (*A. calceolaris* was not examined) have unique flattened scales on the valve (see 133, Character analysis) and *A. ahenea* (and maybe *A. meretricia* and sp.

A) is the only argyrogrammatine to have discrete edges to the dorso-lateral hair tufts on both segments A5 and A6 (79).

Agrapha [ahenea] shares two character states with *Argyrogramma* (a distally dilated uncus, 98, and a long inner tuft in the sternal hair pencil, 88) that must be interpreted as convergent. The hook-like harpe (149), referred to above in connection with *Dactyloplusia* and *Trichoplusia*, is present in *A. ahenea* and *A. meretricia* but in sp. A, the harpe is 'normal' (state 0) but with a small apical point. All species of *Agrapha*, with the possible exception of *A. calceolaris*, have very long antennae (although this is difficult to quantify). I consider the recent inclusion of *Trichoplusia oxygramma* in *Agrapha* by Franclemont & Todd (1983) to be incorrect as this species has none of the autapomorphies of *Agrapha* just enumerated. Similarly, I reject their synonymy of *Ctenoplusia* and *Acanthoplusia* with *Agrapha*. No evidence was found in this study to suggest that these three genera form a monophyletic unit.

Agrapha is the only argyrogrammatine genus wholly endemic to the New World, being found from Costa Rica to Peru. *A. calceolaris* and a possibly undescribed species (not sp. A, may or may not be sp. B) occur on Jamaica. Nothing is presently known about the biology of any of the species but they appear to be widespread through a range of altitudes. *A. meretricia* is recorded from 320 ft (100 m) in Colombia to 6500+ ft (2000+ m) in Peru. Most specimens in the BMNH collection have been taken above 2500 ft (750 m).

Clade 15 [*92(3)*, 144(0)]. The five genera of this clade are united solely on the basis of their possessing an attenuate and dorsally recurved sub-basal lobe on the lateral arms of St8 (92). The degree of development of the clavus (144) has already been shown to be a worthless character (see Character analysis).

Clade 16: *Ctenoplusia* s.l. [*4(2)*, 60(1), 77(1), 119(1), 133(1), *197(1)*]. Given that blade-like saccular setae (133) and a pleurite partially fused with the VAVB (119) are interpreted as convergently derived in this clade and in *Plusiotricha*, only two good synapomorphies were found to unite *Ctenoplusia* and *Acanthoplusia*: the tendency for the pink forewing terminal line to be concentrated at the apex of vein M_3 (4) and the totally desclerotized, membranous antrum (197). The former is by no means universal in *Ctenoplusia* but does occur (or its more derived state 3) in *C. limbirena, C. amydra* Dufay, *C. accentifera* and the *C. furcifera* (Walker) species-complex. This corroborates the hypothesis that *Acanthoplusia* is the sister-group of a section of *Ctenoplusia* and supports Ichinosé's (1973) synonymy. The occurrence of the desclerotized antrum in other species of *Ctenoplusia* and *Acanthoplusia* needs to be confirmed.

Acanthoplusia [83(3), 84(0), 108(0), 214(0)]. *Acanthoplusia* was erected by Dufay (1970*b*) to accommodate five species: *A. tarassota* (Fig. 53) (NE. Himalaya, Java, Bali), *A. ichinosei* (Dufay) (Japan), *A. agnata* (China, Japan), *A. latistigma* (Prout) (Ceram) and *A. eugrapha* (Hampson) (New Guinea). Subsequently, other species were included (Dufay, 1970*b*; 1974; 1982): *A. adiaphora* Dufay (Taiwan), *A. herbuloti* Dufay (Luzon, Philippines), *A. sigillata* Dufay (Luzon, Philippines) and *A. vermiculata* (Sumatra). These species differed from *Ctenoplusia* in the number of cornuti, the shape of the male tergites of segments A5 and A6, and the presence of a pad of inflated scales on the outside of the valve. The first two characters were found to be too variable within the Plusiinae as a whole to be satisfactorily coded in the present study but may have value in a species-level investigation. The scale pad is, however, a good and easily recognizable apomorphy for *Acanthoplusia*, which is doubtless a monophyletic taxon, even if not finally deserving full generic status.

Three species are known from immature stages: *A. tarassota, A. ichinosei* and *A. agnata*. All three appear to be somewhat polyphagous (Ichinosé, 1962*b*; Miyata, 1983). The larvae of *A. agnata* are unusual in the Argyrogrammatini in completely lacking prolegs on segments A3 and A4, instead of bearing vestigial, peg-like structures (Ichinosé, 1962*b*; Eichlin & Cunningham, 1978). All species of *Acanthoplusia*, except *A. agnata* and *A. latistigma*, have a similar, very finely reticulate, brown forewing pattern.

***Ctenoplusia* (s.str.)** [*4(3)*, 60(2), *78(2)*, 86(0)]. As mentioned above (Character analysis, character 60), *Ctenoplusia* (s.str.), as currently constructed, is probably a polyphyletic assemblage of those species with blade-like saccular setae (and some that lack them) that are not members of *Acanthoplusia* or *Plusiotricha*. The last genus shares a similar form of basitarsal comb not found in *Acanthoplusia* (see character 60, Character analysis), while the conspicuous pink forewing spot appears to be a potential synapomorphy for *C. limbirena* (Fig. 54) and several other species (see character 4, Character analysis). The distribution of dorso-lateral tufts that are enclosed in a pleural fold (78) needs to be checked across a wider range of species.

Of the 50 or so species of *Ctenoplusia* (s.str.), the life histories of only two appear to have been elucidated. *C. limbirena*, like many plusiines, is polyphagous, feeding on *Althea* (Malvaceae), *Becium,*

Salvia (both Lamiaceae), *Primula* (Primulaceae), *Verbascum* (Scrophulariaceae), *Solanum* and *Nicotiana* (both Solanaceae) (Pinhey, 1975). In contrast, *C. albostriata* (which is possibly not congeneric with *C. limbirena*) is apparently restricted to members of the Asteraceae (Gardner, 1947; Robinson, 1975; Miyata, 1983; Holloway, 1985), although there are records for *Calystegia* (Convolvulaceae) (Miyata, 1983) and *Symphytum* (Boraginaceae) (Holloway, 1985). Further support for a close relationship between *C. albostriata* and *Trichoplusia vittata* and *T. oxygramma* (see 60, Character analysis) is provided by Pinhey's (1975) record of *Commidendron* (Asteraceae) as the foodplant of *T. vittata* (as *transfixa*) and Crumb's (1956) records of *Aster, Solidago, Erigeron* (Asteraceae) and *Nicotiana* as foodplants of *T. oxygramma*. In *C. albostriata*, a form is known (f. *innotata*) in which the modified Y-mark is missing. The genetics of this and the typical form (f. *albostriata*) was investigated by Ichinosé *et al.* (1967). The two forms were found to obey Mendel's laws of heredity, with f. *albostriata* being totally dominant to f. *innotata*.

Clade 17 [61(1), 83(4), 87(0), 138(0)]. *Plusiopalpa, Stigmoplusia* and *Argyrogramma* are united as clade 17 on the basis of character 61(1), a suppressed inner SV row of setae on the male foretarsi. This state is, however, convergently derived in *Plusiotricha*.

Plusiopalpa [12(1), *41(1)*, 84(0), 86(0), 91(1), 128(1), 201(1), 213(2)]. *Plusiopalpa* is a compact genus of five species that have an unmistakable general appearance. In addition to large size and a somewhat distinctive colour pattern, their most obvious feature is that which has given the genus its name, the very long labial palps. This is due to the extreme dorso-apical elongation of the third segment (41, see Character analysis). In addition there are numerous generic autapomorphies of the genitalia of both sexes including a scimitar-shaped valve, vinculum arms with a marked dorsal keel and medial constriction, and a distinctive corpus bursae in which the ductus seminalis arises from a small apex produced laterally about halfway down the corpus bursae, near the point of entry of the ductus bursae.

Plusiopalpa occurs throughout the Old World tropics. *P. thaumasia* Dufay and *P. hildebrandti* (Saalmüller) are endemic to Madagascar, while *P. shisa* appears to be restricted to Taiwan. *P. adrasta* ranges throughout the Oriental tropics to New Guinea, and *P. dichora* (Fig. 58) occurs in Africa. Hampson's (1913) synonymy of *P. adrasta* and *P. dichora*, followed by Gaede (1940) and Pinhey (1975), is incorrect (Dufay, 1970*a*), while the separation of *P. shisa* from *P. adrasta* ought to be confirmed by genitalic dissection. At present, the only diagnostic characters are minor wing pattern elements. Hampson (1913) also included a sixth species in *Plusiopalpa, P. camptogamma* (Hampson). Dufay (1970*a*) disagreed with this placement but did not suggest a better one. Examination of the genitalia of the female holotype showed that it does not possess the characteristic form of the corpus bursae referred to above that is found in other plusiopalpas, but has a simple corpus bursae instead. Thus *P. camptogamma* should be removed from *Plusiopalpa*. Dufay (unpublished combination in BMNH collection) has proposed that the species is properly placed in *Ctenoplusia*, and the possession by the male of a quadrisetose basitarsal comb (see Character analysis) supports this move. However, examination of the male genitalia is required to confirm this placement as correct. Only *P. adrasta* has ever been reared, from *Mikania*, an asteraceous plant introduced into Peninsular Malaysia (Holloway, 1985).

Clade 18 [*60(3), 61(2),* 79(3), *85(1), 90(1), 92(2), 93(3), 94(3),* 130(0), 162(1)]. Although outwardly different in general appearance, *Argyrogramma* (s.str.) and *Stigmoplusia* share a remarkable number of synapomorphic features, all of which are probably secondary sexual characteristics of the males. These are: a basitarsal comb composed of multiple rows of setae (60); a further suppression of the foretarsal SV spines (61); dorso-lateral hair tufts with discrete edges on segment A6 only (79, but see *Agrapha* and *Stigmoplusia*); differentiated sternal hair pencil insertions (85); an anterior flange on the lateral arm of St8 at the point where they curve dorsally over the hair pencils (90); lateral arms of St8 with the sub-basal lobe modified into a blunt projection (92); dorsal arms of St8 that run almost transversely (93); and apical scales on the dorsal arms of St8 modified into a semicircular, projecting plate (94).

***Argyrogramma* (s.str.)** [*61(3), 78(3),* 88(1), 98(1), 105(1), 108(0), 121(2)]. The members of the genus *Argyrogramma* (s.str.) are most easily recognized by a feature of the male genitalia – the vinculum arms bear broad dorsal and ventral flaps that are folded horizontally and partially fused together to give a stocky, rectangular saccus that is markedly truncate anteriorly (e.g. *A. signata*; Dufay, 1970*a*: fig. 96). In this study, two autapomorphies were found for *A. verruca*, characters 61 (completely suppressed male foretarsal SV spines; short, stout V spines) and 78 (dorso-lateral hair tufts on A7 enclosed in a membranous fold). Two further character states (88, 98) were shared only with *Agrapha* (q.v.) and one only with *Abrostola* (121). Their occurrence in the other members of the genus needs confirmation.

Argyrogramma (s.str.) currently contains 12 species. However, when first described (Chou & Lu, 1978; 1979*a*), five were placed in *Argyrogramma* in the broad sense (i.e. sensu Ichinosé, 1973). These species are

more likely to prove to be ctenoplusias or thysanoplusias and I will not consider them further. *A. circumscripta* does not agree with the type species, *A. verruca*, either. However, Kostrowicki (1961), who transferred *circumscripta* to *Argyrogramma*, had a very peculiar concept for the genus and this species also probably belongs elsewhere. Similarly, *A. aenofusa* was transferred to *Argyrogramma* (s.l.) by Chou & Lu (1978). However, this species does share a potential apomorphy with *A. verruca*, namely a basitarsal comb composed of multiple rows of setae (60:3, see Character analysis). Thus, for the moment, I will leave *A. aenofusa* in *Argyrogramma* (s.str.), despite numerous other differences (e.g. highly modified, spatulate saccular setae).

The core of *Argyrogramma* (s.str.) can thus be considered to consist of five species. Of these, *A. hainanensis* Chou & Lu is almost certainly synonymous with *A. signata*, a widespread species in the Old World tropics, found from the Canary Islands, through to Tonga and the Cook Islands (Dufay, 1970*a*; Holloway, 1985). *A. subaerea* Dufay is recorded from widely scattered localities in tropical Africa from the Ivory Coast to Uganda and SW. Angola (Dufay, 1972), while *A. verruca* (Fig. 59) and *A. basigera* occur throughout North America and Mexico, with the former extending down to Peru and Argentina (Eichlin & Cunningham, 1978), even reaching the Galapagos Islands (Hayes, 1975).

The larvae of both *A. verruca* and *A. basigera* have been described by Eichlin & Cunningham (1978). The former is polyphagous while the larval hostplant of the latter has not been recorded. Although the immature stages of *A. signata* have not been described, Holloway (1985) stated that the species has been reared on *Eucalyptus* in New Guinea. Given that most plusiines feed on herbaceous plants, this record requires confirmation as a natural hostplant.

Stigmoplusia [11(1), *79(2)*, 83(3), 97(1), *111(1), 112(2)*, 144(1), 214(0)]. Three synapomorphies were found for *Stigmoplusia chalcoides* in the present data set: discrete edges to the dorso-lateral hair tufts on segment A5 only (79) and a vinculum produced as a long spine (111; similar to the condition found in clade 8, q.v.), bearing two sharp, subdorsal points (112). There are also several autapomorphies not contained in the data set, including a highly differentiated sternal hair pencil comprising several types of scales (Fig. 270); broad, subventral flaps on the uncus (Figs 280, 281); uncus apically rounded-triangular in cross-section; and strong, asymmetrical digitations on the ventral edge of the valve, distal to the apex of the sacculus, which terminates in a stout, curved spine (Fig. 353).

Seven species are currently placed in *Stigmoplusia*, all described by Dufay (1970*a*; 1972; 1975): *acalypta, allocota, antsalova, chalcoides* (Fig. 60), *epistilba, megista* and *paraplesia*. All except *S. acalypta* and *S. megista* possess uncal flaps. In addition to *S. chalcoides*, valve digitations are present in *S. allocota, S. acalypta* and *S. megista*, but occur along the entire ventral edge of the valve, each digitation bearing a single, short, apical seta. *S. epistilba* and *S. paraplesia* have simple valves, while those of *S. antsalova* are very peculiar (see Dufay, 1970*a*: fig. 109); the apex is enlarged with a basally-oriented, rounded lobe that bears an apical membranous sac. As far as can be ascertained, all species have vinculum arms with subdorsal, sharp points. *Stigmoplusia* thus presents quite a diverse array of male genitalic structure. The females of only three species are known (*S. chalcoides, S. allocota, S. acalypta*) and all agree in the apex of the corpus bursa being ornamented internally with a conspicuous, sclerotized, reticulate pattern of ridges.

Nothing is known about the biology of any species of *Stigmoplusia*. The genus is found in the tropical forest belt of Africa from Liberia to Uganda and Zimbabwe. *S. antsalova*, with the unusual male genitalia, is endemic to west Madagascar.

Clade 19: Plusiini [117(1), 121(1), 127(1)]. The members of the primarily Holarctic tribe Plusiini are united by the synapomorphic possession of a broad flange on the pleurite (117). This structure is, however, subsequently lost in the highly autapomorphic *Antoculeora*. A juxta with an apical notch (or subsequent derivation) (127) is also characteristic of this tribe, although it is lost in *Allagrapha* and convergently derived in *Omorphina* and *Chrysodeixis*.

The larvae of the Plusiini are characterized by the total loss of the prolegs on segments A3 and A4 (but these are also convergently lost in *Acanthoplusia agnata*, see above). There also appears to be a greater degree of larval oligophagy in the Plusiini, but this may be due solely to a lack of information for many (particularly non-pest) members of the Argyrogrammatini.

Clade 20: Euchalciina [39(1), 83(0), *101(1), 178(2)*]. The genera of the plusiine subtribe Euchalciina are characterized by two good synapomorphies: the pleural pouch is small and concealed within the tympanal hood (178) and all have a distinctive outline to the tegumen in lateral view (101). In addition, the sternal hair pencils are invariably reduced to a mere sparse tuft of scales (83), although this reversal to the plesiomorphic condition has also taken place in other genera (*Pseudoplusia, Eutheiaplusia, Syngrapha*). Finally, labial palps in which the ventral scales form a neat ridge (39) are also characteristic of the

Euchalciina, but the condition appears to have been lost in *Euchalcia* and *Adeva* (clade 25). Most of the euchalciines feed as larvae on Ranunculaceae, which may prove to be a further synapomorphy for the subtribe.

Eosphoropteryx [175(1), *213(1)*]. *Eosphoropteryx* is a monobasic genus, comprising *E. thyatiroides* (Fig. 61). It has a number of genitalic autapomorphies, including a keel-shaped valve with a produced apex; an unsclerotized, sub-basal auricular cornutus on the vesica (175; similar cornuti occur in *Macdunnoughia* and *Loboplusia*, but are heavily sclerotized in these genera); a flattened, laterally curved, heavily sclerotized antrum (Fig. 452); and granular ridges on the apex of the corpus bursae (213).

E. thyatiroides is a pinkish-grey plusiine, found across the northern United States and southern Canada, from Nova Scotia and Virginia to British Columbia and Oregon (Eichlin & Cunningham, 1978). The larva is reported to feed on *Thalictrum* (Ranunculaceae) (Forbes, 1954) but no other details of the species' biology are known.

Clade 21 [109(1), *147(1)*, 196(1)]. The remaining genera of the Euchalciina, excluding *Eosphoropteryx*, are united primarily by the synapomorphic shape of the valve (147). The simple, oval valve occurs only in clade 21, with the exception of a convergent occurrence in *Omorphina* (q.v.). As noted above (Character analysis), the valve of *Euchalcia variabilis* is more quadrate than oval, but the majority of euchalcias show the oval valve form. An S-shaped vinculum apex in lateral view (109) is weakly expressed in this clade and also occurs in clade 39 (Plusiina part) and in *Cucullia*. A broad, shallow, open, bowl-like antrum (196) is also characteristic of all members of clade 21 but is highly homoplasious, occurring additionally in *Agrapha* and clade 8 within the Plusiinae and in *Diloba, Cucullia* and *Chalcopasta* in the outgroups.

Polychrysia [5(1), 41(1), 50(1), *65(2)*, 165(1)]. One unique and unreversed apomorphy for *Polychrysia* was found in the present data set; the presence of a few, fine SD and D setae on the tarsi (65). It is unknown if this character state is present in the other members of the genus. *Polychrysia* also possesses scattered black forewing scales (5), an elongate labial palp segment 3 (41) and erect tegulae (50), all of which occur (homoplasiously) only in the Euchalciina (with the exception of the first, which is also found elsewhere in the Plusiini). The subapical cornutus borne on a lateral diverticulum (165) may represent another apomorphy for the genus. The superficially similar condition seen in *Diachrysia* is almost certainly not homologous.

Polychrysia currently contains six species. The most widespread is *P. moneta* (Fig. 62), known in Britain as the Golden Plusia. It occurs across Canada from Ontario to Alberta, and north to Alaska, but has yet to be recorded from British Columbia or east of Lake Huron (Eichlin & Cunningham, 1978). Widely distributed in Europe, *P. moneta* is replaced east of the Urals by *P. esmeralda* (Oberthür). This species differs from *P. moneta* in the silver-grey ground colour to the forewing, rather than a golden-yellow, and has only recently been reinstated as a good species (Kostrowicki, 1961; Chou & Lu, 1979*a*). However, there is some confusion (compare the figures of the male genitalia in the above two publications) and the separation of *P. esmeralda* from *P. moneta* is still open to question.

P. sica, P. aurata (Staudinger) and *P. splendida* (Butler) are all eastern Palaearctic (China, Japan, Siberia) (Kostrowicki, 1961), while *P. morigera* (Edwards) is restricted to the foothills of the Rocky Mountains of the U.S.A., both the eastern and western slopes. '*Polychrysia*' *aureus* (Bang-Haas) (Kostrowicki, 1961) is not a plusiine but is correctly assigned to the amphipyrine genus *Chrysonicara* Draudt, near *Nicara* Moore (Draudt, 1937).

The life history of *P. moneta* in Europe is well known (Bretherton *et al.*, 1983). The larvae are most frequently recorded feeding on members of the Ranunculaceae; e.g. *Aconitum, Delphinium* (South, 1961; Skinner, 1985) and *Trollius* (Beck, 1960; Kostrowicki, 1961). However, the last author also gives *Cucumis* (Cucurbitaceae) and *Helianthus* (Asteraceae), while South (1961) adds *Arctium* (Asteraceae). *P. splendida* appears to be restricted to *Aconitum* (Miyata, 1983), while *P. morigera* is recorded only from *Delphinium* sp. (Eichlin & Cunningham, 1978). Pupation is in a characteristic strong, oval cocoon of yellow silk spun between leaves of the foodplant (Bretherton *et al.*, 1983).

Clade 22 [3(0), 154(1), 183(1)]. The members of clade 22 are primarily characterized by short anal papillae (183). However, as noted above (Character analysis), *Euchalcia variabilis* exhibits the plesiomorphic condition of approximately square papillae and this was interpreted as an early stage in a transformation series culminating in the blade-like papillae of species such as *E. augusta*. Transtillae that are fused above the aedeagus into a broad, blunt point (154) also characterize clade 22, with the exception of the included clade 26. Further investigation may show this character state to be a synapomorphy of clades 23 and 25.

Clade 23 [42(1), *132(1), 163(1)*]. Two synapomorphies unite *Panchrysia* and *Chrysanympha* into a monophyletic group: fused saccular flanges modified into a rounded lobe between the valves (132) and an apically swollen subapical cornutus (163). However, the latter appears to be present in *Panchrysia* only in *P. deaurata, P. ornata* (Bremer) (Kostrowicki, 1961; Chou & Lu, 1978) and *P. mishanensis* Chou & Lu (Chou & Lu, 1979*a*), while the former may be of more general occurrence, being distinguishable in figures of the genitalia of *P. deaurata, P. ornata* and *P. dives* but not *P. v-argenteum* (Esper) (Kostrowicki, 1961) or *P. mishanensis* (Chou & Lu, 1979*a*). The sister-group relationship of *Panchrysia* and *Chrysanympha* therefore remains equivocal.

Chrysanympha [5(1), 41(1), 107(1)]. *Chrysanympha* contains a single species, *C. formosa* (Fig. 63), of unique general appearance within the Plusiinae. The forewing has a strong, brown, evenly-curved subterminal line and the pinkish grey colour of the Y-mark is extended costally and basally to give a superficially similar pattern at the wing base to *Abrostola* (into which genus *C. formosa* was incorrectly placed by Hampson, 1913). *Chrysanympha* also bears a dorsal sclerotized bar on the anal tube (107), similar to that seen in *Lophoplusia* and the Abrostolini, and is another euchalciine to display scattered black scales on the forewing (5).

C. formosa appears to be a scarce species confined to the north-eastern U.S.A. and south-eastern Canada (Eichlin & Cunningham, 1978). Its life history has been briefly described by Kearfott (1904) and the larval foodplants are given as *Gaylussacia* and *Vaccinium* (Ericaceae) (Tietz, 1972), unusual for the Euchalciina.

Panchrysia [19(1), 65(3), 209(1)]. *Panchrysia deaurata* is the only euchalciine to my knowledge in which the ductus seminalis arises from the fundus of the corpus bursae (209). This may prove to be an autapomorphy for the species, as the ductus seminalis has the more usual origin from the apex of the corpus bursae in *P. ornata* (Chou & Lu, 1978: fig. 23). Like *Polychrysia, Panchrysia deaurata* has SD and D tarsal setae (65) but in the present genus, they are numerous and long, much as in the distantly related *Lophoplusia*. The presence of this character state in the other members of the genus needs confirmation.

Five species currently comprise *Panchrysia*. The type species, *P. deaurata* (Fig. 64), is found in steppe and semi-arid areas of Europe and Central Asia from Spain to the Altai. It is a golden-yellow moth, superficially(?) similar to *Polychrysia aurata*, and thus unlike the other members of its genus in general appearance. The other four species all bear a silver Y-mark and other metallic spots on the forewings. *P. v-argenteum* (Fig. 65) is a pinkish brown moth restricted to the European Alps and the high mountains of south-east Europe (e.g. Yugoslavia, Greece), while *P. ornata* is very similar but pale grey-brown. The latter species occurs in the eastern Palaearctic steppes (Kostrowicki, 1961), and thus stands in relation to *P. v-argenteum*, in terms of both distribution and colour, much as *Polychrysia esmeralda* stands in relation to *Polychrysia moneta*. *Panchrysia mishanensis* is very similar to *P. ornata* (Chou & Lu, 1979*a*) and presumably originates from Mi-Shan in far north-eastern China, but this is not certain. The fifth species, *P. dives* (Fig. 66), is similar to *P. v-argenteum* but the forewing is chocolate-brown, has more extensive silver markings, and the hindwing is yellow with a brown margin. It is largely sympatric with *P. ornata*, but extends further east into southern Kamtchatka and is absent from the Korean peninsula and most of China (Kostrowicki, 1961).

Little is known of the biology of *Panchrysia*. The larval foodplants of *P. deaurata* are recorded as numerous species of *Thalictrum* (Ranunculaceae), while *P. v-argenteum* feeds on *Isopyrum* (Ranunculaceae), as well as *Thalictrum foetida* (Kostrowicki, 1961).

Clade 24 [6(0), 144(1), *168(1)*, 205(1)]. The five genera comprising clade 24 are united by the synapomorphic possession of a vesica that is internally granular basally (168).

Clade 25 [*4(4)*, 39(0), 58(0), *164(1)*]. *Euchalcia* and *Adeva* are considered sister-taxa on the basis of two synapomorphies. In both genera, the terminal line on the forewing is white not pink (4) and the subapical cornutus on the vesica arises from a circular, concave base-plate (164). These two character states also occur in all other *Euchalcia* species represented in the BMNH collection or figured by Dufay (1968), with the following exceptions. The white terminal line is absent in *E. inconspicua* (Graeser) (Fig. 69), *E. cashmirensis* Moore and *E. dorsiflava*, and is reduced in several other species. The circular base-plate of the subapical cornutus is absent only in *E. inconspicua*, where the subapical cornutus is replaced by a series of cornuti, and *E. tancrei* (Staudinger). Dufay (1968) considered *Euchalcia* to be a very homogeneous genus, in terms of general facies and male and female genitalia, providing *E. inconspicua, E. tancrei* and 'Plusia' *hampsoni* Leech (Fig. 68) were excluded (all were first transferred to *Euchalcia* by Kostrowicki, 1961, the last as its synonym, 'Phytometra' *lenzeni* Draudt [Dufay, 1965]). *Euchalcia inconspicua* has

recently been placed in its own genus, *Pseudochalcia*, by Kljutshko (1984). I have examined the male genitalia of *hampsoni* (BM noctuid slide no. 11521) and agree with Dufay (1968) that this species does not belong in *Euchalcia*. I am unable at present, however, to suggest where 'P.' *hampsoni* ought to be placed. I superficially examined specimens of *Euchalcia tancrei*, together with the drawing of the male genitalia in Kostrowicki (1961), and I concur with Dufay that this species, also, does not belong in *Euchalcia*. Although it is unsatisfactory, until such time as a more comprehensive study is performed, both *hampsoni* and *tancrei* should be placed in limbo (i.e. 'Plusia' s.l.). This action, together with the removal of *inconspicua* to *Pseudochalcia* (see also Consensus classification), almost certainly leaves *Euchalcia* (+ *Adeva*) monophyletic.

Euchalcia [183(0), 201(0)]. The genus *Euchalcia* comprises around 30 species. They are found almost exclusively in the steppe and semi-arid regions of the Palaearctic, the exceptions being *E. cashmirensis*, *E. serraticornis* Dufay and *E. xanthoides* Dufay, which are subtropical-Himalayan species (Dufay, 1968). *Euchalcia gerda* and *E. serraticornis* have serrate male antennae (the females are unknown for both species), and are thus somewhat unusual (Dufay, 1968).

The biology of only seven species is known (Dufay, 1968). *E. variabilis* (Fig. 67) and *E. bellieri* (Kirby) are reported to feed as larvae on the usual ranunculaceous foodplants of the Euchalciina, *Aconitum* and *Thalictrum*. However, one group of euchalcias has undergone a foodplant switch to members of the Boraginaceae: *Alkana* (*E. chlorocharis* (Dufay)), *Cynoglossum* (*E. cuprea* (Esper) and *E. italica* (Staudinger)), *Lycopsis* (*E. consona* (F.)), *Pulmonaria* (*E. consona* and *E. cuprea*), *Rindera* (*E. siderifera* (Eversmann)), *Nonea* (as *Nonnea*; *E. consona*) and *Symphytum* (*E. cuprea*) (Beck, 1960; Kostrowicki, 1961; Dufay, 1968). In addition, *E. cuprea* is recorded from *Pterotheca* (Asteraceae) and, most unusually, *Arum* (Araceae) (Kostrowicki, 1961).

A comprehensive revision of the genus has been provided by Dufay (1968), including detailed accounts of the morphology, distribution and affinities of 29 species of *Euchalcia* and separate keys to species using general habitus, male and female genitalia.

Adeva [5(1), 59(0)]. *Adeva* is yet another euchalciine to have scattered black scales on the forewing, and in this character state, the sole included species, *A. albavitta*, differs from all species of *Euchalcia* that I have examined.

Adeva was erected by McDunnough (1944) to accommodate *A. albavitta* (Fig. 71). The genus was considered synonymous with *Euchalcia* by Kostrowicki (1961), a decision endorsed by Dufay (1968). *A. albavitta* is restricted to the south-western U.S.A., where it occurs in the states of Oregon, California, Arizona and Nevada (Eichlin & Cunningham, 1978). There are two colour forms, a pale brownish form found in the coastal regions of California, and a smoky grey desert form, originally described in the genus *Behrensia* Grote (McDunnough, 1944). Nothing is known about the biology of *A. albavitta*. However, given the dichtomy in *Euchalcia* of larval foodplants between the Ranunculaceae and the Boraginaceae, knowledge of that of *Adeva* might prove useful in resolving the position of this species with regard to the 30 or so euchalcias.

Clade 26 [144(2), 154(0), *171(1), 186(1), 194(2)*]. *Plusidia, Lamprotes* and *Pseudeva* form a monophyletic group on the basis of three synapomorphies: the presence of an isolated, dorsal patch of cornuti on the vesica (171); short, thick membrane preventing easy protraction of the anal papillae (186); and the presence of several setae along the inner, ventral edge of the antrum (194). This last character state is further transformed in *Lamprotes* (q.v.) and a superficially similar but non-homologous condition occurs in *Diloba*.

Plusidia [58(0)]. *Plusidia* currently contains three species. However, *P. imperatrix* and *P. chinghaiensis* Chou & Lu show considerable similarities in wing pattern to *Polychrysia splendida* and examination of the genitalia may show that they are properly placed in *Polychrysia*.

This action would render *Plusidia* monotypic, containing only *P. cheiranthi* (Fig. 34). At one time, the eastern Palaearctic populations were considered to be a separate species, *P. separanda* Warren (Inoue & Sugi, 1958–61). More recently, it has been relegated to subspecies of *P. cheiranthi* (Kostrowicki, 1961) and finally considered to be fully synonymous (Sugi, 1982).

Western populations of *P. cheiranthi* are unmistakable in appearance. The forewings are pinkish grey, with a chocolate-brown, comma-shaped apical spot and a similar brown spot at the base. However, eastern examples have a much more 'washed-out' appearance with the apical spot barely distinguishable and the basal spot often somewhat faded also. The larva was briefly described by Kirby (1889), who gave the foodplants as *Thalictrum* and *Aquilegia* (Ranunculaceae).

Clade 27 [6(1), 16(1), 19(1), 41(1), 42(1), 205(0)]. There are no good synapomorphies to support the sister-group relationship between *Lamprotes* and *Pseudeva*, which must thus be considered tentative at best. Nevertheless, this relationship has been proposed previously by Kostrowicki (1961), who stated that *Lamprotes* was 'in facies and genitalia much like the species of the Nearctic genus *Pseudeva*' (see also *Pseudeva* below).

Lamprotes [3(1), 144(1), 162(0), 191(1), *194(1)*, 201(1)]. *Lamprotes* can be separated from the other two genera of clade 26 by the restriction of the ventral antrum setae to a subventral or lateral position (194). In addition, most *Lamprotes* specimens bear a small, golden, C-shaped mark below the forewing cell (3). This marking was coded in the data as homologous with the Y-mark of other plusiines. However, the C-mark of *Lamprotes* occupies a slightly more basal position (entirely below vein CuA_2 rather than straddling it) and this suggests that it represents a novel pattern element that is autapomorphic for *Lamprotes*.

Lamprotes has a very similar disjunct distribution to *Plusidia*, with western and eastern Palaearctic populations. However, in contrast to that genus, the eastern population of *Lamprotes*, *L. mikadina* Butler, has long been treated as a good species (Hampson, 1913; Inoue & Sugi, 1958–61; Chou & Lu, 1979*a*; Sugi, 1982). Occasionally, *L. mikadina* has been treated as a subspecies of *L. c-aureum* (Kostrowicki, 1961) (Fig. 35), or even fully synonymized (implicitly in Forster & Wohlfahrt, 1971).

The larva of *L. c-aureum* has been briefly described by Kirby (1889) and that of *L. mikadina* in more detail by Ichinosé (1962*b*). Both species are reported to feed on *Thalictrum* and *Aquilegia*.

The generic name *Lamprotes* is unusual insofar as the identity of the author is unknown, only his or her initials accompanying the first reference to the name (R.L., 1817). According to W. H. T. Tams (Nye, 1970; unpublished notes), the identity of R.L. was investigated by C. D. Sherborn. However, he reached no firm conclusion. C. Boursin has attributed authorship to Reichenbach of Leipzig, but it could also be Rudolph Leuckhart (who published under his own name 1836–1859) or Rudolph Ludwig, suggested by E. L. Todd (Nye, 1970; unpublished notes). Nye suggested that continuing to use R.L. was the most prudent course.

Pseudeva [5(1), 50(1)]. *Pseudeva* contains only two species, *P. purpurigera* (Fig. 36) and *P. palligera*. Both species, like *Polychrysia*, have erect tegulae (50). However, this character state is difficult to score in any specimen that is little less than perfect and may yet be shown to occur in other euchalciine genera.

Both species of *Pseudeva* are endemic to the Holarctic region. *P. palligera* occurs only in the south-western U.S.A., while *P. purpurigera* is widespread in southern Canada and the northern two-thirds of the U.S.A., east of the Rocky Mountains, but is noticeably absent from the central band of states from North Dakota to Texas.

The larva of *P. purpurigera* has been described by Dyar (1896), who gave *Thalictrum* as the foodplant. He also stated that the larva was 'green and white [and] curiously hunched up'. This description is very similar to the coloration and posture of the larva of *Lamprotes mikadina* (Ichinosé, 1962*b*: pl. 18, fig. 4; Mutuura *et al.*, 1965: pl. 37, fig. 113) and these features may represent good synapomorphies for *Lamprotes* and *Pseudeva*. Further examination of the larvae of *Pseudeva* is thus important in confirming the sister-group relationship of these two genera.

Clade 28 [116(1)]. The subtribes Plusiina and Autoplusiina are interpreted as sister-taxa solely on the basis of a strongly curved pleurite (116). As noted earlier, such a structure also occurs in *Anadevidia* and thus the monophyly of clade 28 can only be considered to be weakly supported. Eichlin & Cunningham (1978) treated the Plusiina and (paraphyletic) Euchalciina as sister-taxa on the basis of a shared fusion of the pinacula of setae SV1 and SV2 on segment A2 of the larva. However, this character state also occurs in several non-Nearctic autoplusiine genera (*Macdunnoughia*, *Sclerogenia* and *Erythroplusia*), as well as in the argyrogrammatines *Thysanoplusia* and *Anadevidia* (Ichinosé, 1962*b*), and is thus of dubious value.

Clade 29: Autoplusiina [18(0), 213(2)]. The members of the Autoplusiina are only weakly united as a monophyletic group on the basis of sclerotized ridges at the entry point of the ductus bursae into the corpus bursae and on the apex of the corpus bursae (213). However, these ridges must have been secondarily lost in *Erythroplusia*. In addition, such ridges occur in *Omorphina* and *Plusiopalpa* within the Plusiinae, and in *Diloba* and *Chalcopasta* of the outgroups. Further study is required into this character and, given the reservations regarding the homologies of other character states important in the classification of this subtribe (e.g. see Characters, 142: 1 & 2), the Autoplusiina may subsequently be shown to be paraphyletic or worse.

Rachiplusia [14(2), 59(0), *63(1)*, 64(2), 110(1), 114(1), 139(1), 148(0), 154(1), 191(1), *198(3)*, 206(1),

216(1)]. *Rachiplusia* is perhaps the most problematical autoplusiine genus, in that it shares possible synapomorphies with a number of subgroups of the subtribe. *Rachiplusia* and *'Syngrapha' gammoides* are the only autoplusiines that are sexually dimorphic (216), while a bisetose female frenulum (14) and spined hind tibiae (64) further corroborate a relationship between *Autoplusia* and *Rachiplusia*. *Rachiplusia* also shares character states with larger clades that include *Autoplusia*: increased sclerotization of the LPV and T8 ventrally (198: clade 35); lack of a harpe (140: clade 34); and a protected ostium bursae (191: clade 36). This last character is also shared, however, with the members of clade 32, as is a clavus base that is obscured by a saccular overfold (139). Finally, *Rachiplusia* and *Macdunnoughia* s.l. (clade 33) both have a medially expanded section of the ductus bursae with dorsally recurved edges (206). It is thus unlikely that *Rachiplusia* will prove not to be related to some or all of the autoplusiines of clade 30. However, the genus lacks many structures found in this clade, most notably the apomorphic states of characters 95, 141, 189 and 193 (see below). A more extensive survey of the Autoplusiina (and maybe the Plusiina, see *Anagrapha* and *Syngrapha* below) is necessary to resolve these ambiguities.

Rachiplusia comprises three species. Two, *R. nu* (Fig. 72) and *R. ou*. are very similar, both in general appearance and in genitalia. *R. ou* occurs from the U.S.A. south to Venezuela (including Jamaica and the Bermuda Islands), while *R. nu* is found in Bolivia, Chile, Brazil and Argentina. The immature stages of *R. nu* have been described in detail by Angulo & Weigert (1974), and the larvae of *R. ou* by Crumb (1956). Both species are highly polyphagous (Angulo & Weigert, 1975; Eichlin & Cunningham, 1978) but only *R. nu* appears to be of economic importance as an agricultural pest (Angulo & Weigert, 1975).

The third species, *R. virgula*, has long been considered a member of the genus *Caloplusia* (e.g. Hampson, 1913; Kostrowicki, 1961), because of its reduced eyes, yellow hind wings and fully spined tibiae. Following examination of the genitalia, however, Angulo (1978) transferred *virgula* to *Rachiplusia*. There can be little doubt that this reflects the relationships of the species more precisely. Both *R. virgula* and *R. nu* (the second species figured by Angulo, 1978) have a ventrally bulged valve (Fig. 360); long, thin clavi (Fig. 360); a broad, truncate saccus (Fig. 302); and a similar arrangement of cornuti on the vesica. The immature stages of *R. virgula* have been described by Izquierdo (1895), who gave the larval foodplant as *Madia sativa* (Asteraceae). *R. virgula* is endemic to the Chilean Andes.

It does not appear to have been noted before that two of the species of *Rachiplusia* are sexually dimorphic. The males are more brightly and contrastingly coloured than the females, which are dull in comparison. In addition, the males have a predominantly grey forewing ground colour, while the females are brown. A similar but more striking dimorphism occurs in *'Syngrapha' gammoides* (Figs 82, 83). In contrast, *R. virgula* appears to be monomorphic, although I have not seen a sufficiently long series of this species to be certain.

Clade 30 [83(2), 95(1), 141(1), 162(0), 189(1), *193(1)*]. The remaining members of the Autoplusiina, excluding *Rachiplusia*, are united by a single unique and unreversed synapomorphy, the presence of short, upright scales on the antero-ventral margin of the antrum (193). In addition, a broad, triangular saccular spine (141) occurs in many members of the subtribe, although some extreme modifications may eventually prove to be incorrectly homologized (e.g. the quadrate lobe of *Erythroplusia* and the lance-like projection of *Antoculeora*). Fine, hair-like scales ventrally between the lateral arms of St8 (95) occur in all the member genera of clade 30 except *Sclerogenia*, while a T8 that is cut back ventral to the anterior apophysis (189) is present in all but *Antoculeora*, where the extreme autapomorphic condition of the male genitalia make it difficult to score the character. However, the apomorphic state of character 189 also occurs in *Syngrapha* (s.l.) and *Anagrapha* (see below). Again, a more extensive investigation is necessary, particularly of the male genitalia, in order to confirm several of the homologies hypothesised in this study (especially those of characters 141 and 142).

Erythroplusia [5(1), 6(1), 18(1), 104(1), 108(1), 145(1), 155(1), 158(2), 209(1), 213(0)]. Like *Rachiplusia*, the relationships of *Erythroplusia* are somewhat obscure. It also possesses character states that associate it with several different members of the Autoplusiina. Convergent upon the condition found in *Antoculeora*, the tegumen arms of *Erythroplusia*, in dorsal view, diverge at about 180 degrees, rather than forming the more usual inverted V-shape (104). *Erythroplusia* bears its clavus on a long, flattened peninsula (145), as in *Antoculeora* and *Macdunnoughia* (s.l.). As in the latter genus (s.str.), the ventral sclerotization on the aedeagus of *Erythroplusia* is restricted to a very thin, ventral band, convergent upon the condition seen in the Argyrogrammatini. Finally, the form of the transtillae (155) is almost identical to that seen in *Sclerogenia*.

In addition to the above states, the two constituent species of *Erythroplusia* show several other remarkable genitalic autapomorphies. The valves are asymmetrical (Fig. 378). The sacculus of the left valve bears a distally directed, curved process, while that of the right valve bears a subapically recurved,

heavily-sclerotized ridge and no process. The corpora bursae of the females are highly simplified relative to those seen in other autoplusiines. That of *E. rutulifrons* (Fig. 453) is a simple, cylindrical sac, somewhat swollen where it recurves posteriorly through about 180 degrees. There is no obvious differentiation into ductus and corpus bursae. The corpus bursae of *E. pyropia* is more swollen and tapers distally. In both, it is extremely difficult to ascribe the terms apex and fundus with any degree of certainty (see also Characters: 209).

Erythroplusia was originally proposed as a subgenus of *Autographa* (Ichinosé, 1962*a*; *b*). Subsequently, it was elevated to full generic rank (Ichinosé, 1973) and included *Antoculeora* (q.v.) as a subgenus. The precise relationships of *Erythroplusia* are still equivocal. There are some larval characters that suggest a relationship with the Argyrogrammatini (a slender seta SD1 on segment A9 was used by Kljutshko, 1985*a*, to associate the two taxa as sister-groups), while the chaetotaxy is identical in *Erythroplusia* and *Autographa* (which included *Sclerogenia*; Ichinosé, 1973).

The larvae of both species have been described by Ichinosé (1962*b*). No foodplants were given for *E. rutulifrons* but that of *E. pyropia* was stated to be *Artemisia* (Asteraceae). Miyata (1983) gave *Arctium* (Asteraceae) and *Oenanthe* (Apiaceae) for both species. *Erythroplusia* is primarily north-eastern Palaearctic in distribution, with the two species being broadly sympatric over much of their ranges. However, *E. pyropia* extends further west than *E. rutulifrons* (Fig. 73), occurring throughout the southern Himalayan foothills to Kashmir (Kostrowicki, 1961).

Clade 31 [113(1), 142(1), 176(1), 177(1)]. There are no unique and unreversed synapomorphies uniting the seven constituent genera of clade 31. All four of the character states listed above are reversed in one or more genera, and three also occur in the outgroups. Characters 176 and 177 have been discussed in detail earlier; they are reversed in *Loboplusia* and *Puriplusia* respectively, and the former is also present in *Brachionycha*. A saccular sheet (142) is absent in *Loboplusia*, while convergent developments are to be found in *Calophasia, Magusa* and *Lophoptera*. Finally, the form of the vinculum (113) is interpreted as a synapomorphy for clade 31. However, the character is subsequently reversed in the included clade 35, and also occurs in *Anagrapha*. This, together with the uncertainty concerning the homology of states 1 and 2 of 142 and the ambiguity provided by *Loboplusia* (and to a degree *Anagrapha*), suggests that clade 31 may not retain its current topology when further taxa and characters are analysed.

Clade 32 [*99(2)*, 137(1), 139(1), 191(1)]. *Allagrapha* and *Macdunnoughia* (s.l.) are interpreted as sister-taxa primarily on the basis of a produced tegumen apex (99). Also, the setae along the ventral edge of the valve are borne on marginal prominences (137), a condition otherwise only seen in *Omorphina*, where it is associated with a different valve shape. As noted earlier, clade 32 convergently shares a concealed clavus base (139) with *Rachiplusia*. A relationship between *Allagrapha* and *Macdunnoughia* (s.l.) was first suggested by Franclemont (1964).

Allagrapha [3(0), 16(1), 18(1), 58(0), 127(0), 201(1)]. *Allagrapha* is here interpreted as a monotypic genus containing only *A. aerea* (Fig. 75) (McDunnough, 1944; Franclemont & Todd, 1983). Occasionally (e.g. Eichlin & Cunningham, 1978), a second species, *aereoides* (misspelt in McDunnough's (1944) figure captions, Eichlin & Cunningham (1978) and Franclemont & Todd (1983) as *aeroides*), has been included. Eichlin & Cunningham (1978) presented, as evidence for this inclusion, the absence in both species of a raduloid on the larval hypopharynx (present in *Diachrysia balluca*), modifications of the male genitalia and a strong superficial similarity. Ichinosé (1973), however, synonymized *Allagrapha* (as *Agrapha*) with *Diachrysia* (as *Plusia*), noting a unique larval chaetotaxy (his type F) and the well-defined pocket in the female segment A8, discounting the modification to the sacculus in *A. aerea* (Fig. 368).

However, while *aereoides* can remain in *Diachrysia*, I conclude that *aerea* is best retained for the present in the separate genus *Allagrapha*, on the basis of the characters discussed in previous sections. Nevertheless, several *Diachrysia* species do complicate matters. *D. leonina* has a broad, cone-shaped vinculum (113); *D. nadeja* (Oberthür) bears a small, broad, triangular spine on the sacculus (141); and the marginal setae on the valve of *D. chrysitis*, at least, are borne on small prominences (137). A more extensive analysis of *Diachrysia* may eventually show that not only is this genus more closely related to some Autoplusiina than to the Plusiina (as is concluded in the present analysis), but also that *Allagrapha* is merely a divergent species. However, it is unlikely that *A. aerea* and *Diachrysia aereoides* will prove to be sister-species.

In addition to the characters already mentioned, *Allagrapha* also has several genitalic autapomorphies. The harpe is broad, flat and spoon-shaped; the clavus has a markedly swollen apex (Fig. 368); the LHS basal sclerotization on the vesica bears very strong, sharp spines; and the ostium bursae is protected by a large, spiculate lobe.

Allagrapha aerea is an undistinguished brown plusiine, showing, as already noted, strong superficial

similarity in wing shape and pattern to *Diachrysia aereoides, D. leonina* and *D. bieti*. It is widely distributed in southern Canada and the U.S.A., east of the Rocky Mountains (Eichlin & Cunningham, 1978). The larvae are generally polyphagous on low plants (Forbes, 1954) such as *Urtica* (Crumb, 1956), *Aster* and *Glycine max* (Papilionaceae; Eichlin & Cunningham, 1978).

Clade 33: *Macdunnoughia* (s.l.) [145(1), *150(1), 192(1),* 206(1), 213(3)]. The two constituent taxa of *Macdunnoughia* (s.l.), *Macdunnoughia* (s.str.) and *Puriplusia*, share two unique and unreversed synapomorphies: a harpe in the form of an inwardly curving hook (150) and the presence of spinose pads lateral to the ostium bursae (192). Both characters are subsequently transformed, 150 in *Macdunnoughia* (s.str.) and 192 in *Puriplusia*. In addition, and as previously noted, clade 33 convergently shares the apomorphic states of 145, 206 and 213 with *Erythroplusia/Antoculeora, Rachiplusia* and clade 35 respectively.

Puriplusia [177(0), *192(2)*, 209(1)]. *Puriplusia* differs from *Macdunnoughia* (s.str.) primarily in the spinose pads lateral to the ostium bursae being elongated into recurved grooves (192). In addition, the apex of the corpus bursae has rotated through approximately 180 degrees and is thus directed anteriorly (209; see Character analysis). *Puriplusia* also lacks concave lateral edges to the female St7 (177), probably as a consequence of the reduced pleural membrane thickening (176). Autapomorphies not included in the data set are the saccular sheet that is modified into an incurved hook and a sacculus bearing a distinct, blunt spine (Fig. 369). The forewing pattern is also distinctive, although the high contrast two shades of grey seen in typical *P. purissima* is replaced by an almost uniform grey-brown, on which the cross-lines are barely distinguishable, in some forms of *P. tetragona* (Walker) (the synonymous *P. semivitta* (Moore); Dufay, 1977).

There are currently two species placed in *Puriplusia, P. purissima* (Fig. 77) and *P. tetragona*. *P. semivitta* may prove to be a third or merely a colour form of *P. tetragona*. However, the complex is in need of revision and there is at least one undescribed species in the BMNH collection. *P. tetragona* differs most markedly from *P. purissima* in the presence of a row of short, curved cornuti on the vesica, similar to those found in *Macdunnoughia* (s.str.) (see also Ronkay, 1982). Additionally, the recurved spiculate grooves lateral to the ostium bursae are less well developed and there is no black dash above the Y-mark, distal to the forewing discal cell.

P. purissima occurs in China, Korea and Japan (Hampson, 1913). The larva was described by Ichinosé (1960) but no record of the larval foodplant was made. Miyata (1983) gave *Artemisia* and *Arctium* (Asteraceae). *P. tetragona* is found further west and south in India. There are also specimens in the BMNH collection from Taiwan. The undescribed species referred to above is exceptional in being collected from west Sulawesi.

***Macdunnoughia* (s.str.)** [*150(2)*, 158(2), 175(1)]. *Macdunnoughia* (s.str.) is characterized in this data set by the presence of an upward curving spine at the base of the harpe (150). It also bears a characteristic sharp-edged auricular cornutus at the base of the vesica (175) and, like *Erythroplusia* and the Argyrogrammatini, has the ventral sclerotization of the aedeagus restricted to a discrete narrow band (158).

Four species were placed in *Macdunnoughia* (s.str.) (type species: *M. confusa*) by Kostrowicki (1961). Examination of the male genitalia of the holotype of *M. camptosema* Hampson showed that it lacks all the apomorphies listed above for the Autoplusiina and correctly belongs in *Autographa* (**comb. n.**). The male genitalia figured by Kostrowicki as *A. camptosema* (1961: fig. 54) are those of *M. confusa* (cf. his fig. 53). In addition, Ichinosé (1973) has already pointed out that the female genitalia of *M. crassisigna* figured by Kostrowicki are actually also those of *M. confusa*. Thus, Kostrowicki, to whom the male of *M. crassisigna* and the female of *A. camptosema* were unknown, appears to have examined only one species of *Macdunnoughia* (s.str.) (the appropriately named *M. confusa*!) but treated it as three separate species. The last species transferred to *Macdunnoughia* by Kostrowicki was *M. schalisema* (Hampson), although this time he did not examine any specimens. However, I have examined the genitalia of the female holotype of *M. schalisema* and conclude, from its lack of both lateral spiculate pads near the ostium bursae and a strongly ridged apex to the corpus bursae, that the species does not belong in *Macdunnoughia*. Instead, a comparison with the types of *Autographa emmetra* Dufay shows *schalisema* to be extremely similar both in forewing pattern and in female genitalia. I thus transfer *M. schalisema* to *Autographa* (**comb. n.**) and synonymize *Autographa emmetra* (**syn. n.**) with it.

There are therefore only three species remaining in *Macdunnoughia* (s.str.): *M. confusa* (Fig. 76), *M. crassisigna* and *M. monosigna* Chou & Lu. The last of these closely resembles the second in male genitalia and may only be a colour form of *M. crassisigna* in which the basal half of the Y-mark has been lost. As noted above (150: Character analysis), *M. crassisigna* has only a rudimentary upcurving spine at the base of the harpe and is thus intermediate between *M. confusa* and *Puriplusia*. A more crucial feature, however, is

that in *M. crassisigna*, the apex of the corpus bursae is reflexed anteriorly and elongate, as in *Puriplusia purissima*. If this condition is interpreted as apomorphic, and a comparison with the other members of the Autoplusiina suggests that it is, then a sister-group relationship between *M. crassisigna* and *Puriplusia* is indicated, rendering *Macdunnoughia* (s.str.) paraphyletic.

M. confusa is a trans-Palaearctic species ranging from France, across central Europe and Asia, to northern China, Japan and even the southern tip of Kamtchatka (Kostrowicki, 1961). However, until about 1918, the species was only known from eastern Europe. After this date, *M. confusa* began a rapid westward expansion of its range and is now probably resident in Italy, Spain and France. The species was first recorded from Great Britain in 1951 (Dewick, 1951) but never became resident. It appeared to have reached its limits in western Europe by 1955 (Bretherton *et al.*, 1983).

M. crassisigna occurs in China, the Korean peninsula and Japan, extending westward through northern Burma to India and Pakistan (Kostrowicki, 1961), while *M. monosigna* has only been recorded from somewhere in China.

The larvae of both *M. confusa* and *M. crassisigna* have been described by Ichinosé (1958*b* and 1962*b* respectively). Both species appear to be somewhat polyphagous, but with a slight bias towards members of the Asteraceae (Beck, 1960; Kostrowicki, 1961; Ichinosé, 1962*b*; Miyata, 1983). Oord (1985) stated that *M. confusa* larvae fed on *Artemisia* before hibernation and *Lactuca* and *Matricaria* after reawakening in spring.

Clade 34 [12(1), 59(0), 148(0)]. The three character states that unite the four constituent genera of clade 34 are very weak and it is unlikely that future studies will corroborate its monophyly. The main problem is *Loboplusia* (q.v.) with its highly simplified male valves and numerous missing data. This genus is probably not closely related to clade 35 (*Sclerogenia, Autoplusia* and *Antoculeora*).

Loboplusia [6(1), 141(1), 142(0), 144(0), 175(1), 176(0), 209(1)]. *Loboplusia* is perhaps most notable in the present data set for the autoplusiine structures it does not possess. The genus lacks a broad saccular spine (141), a saccular sheet (142), has a reduced clavus (144) (Fig. 371) and, while the lateral edges of St7 in the female are probably concave (177), the pleural membrane is unmodified (176). The genus possesses an auricular cornutus (175), but as the vesica of the slide preparation was not everted, its position on the vesica is only assumed to be basal. Also, like *Puriplusia*, the apex of the corpus bursae is rotated to face anteriorly.

Nevertheless, the male *Loboplusia* has the most remarkable array of autapomorphic scent organs, their diversity exceeding even *Chrysodeixis*. In addition to the usual sternal hair pencils, the hind tibia is considerably swollen and bears a dense dorsal fringe of long, golden hairs. The hind tarsi are similarly adorned but are of normal dimensions. The anal angle of the hindwing is extended into a long lobe (superficially similar to the anal scent fold of swallowtail butterflies), which is folded and contains numerous long hairs. Finally, the outer edge of the hindwing upperside and the basal costal edge of the hindwing underside also bear modified scales. All in all, the male *Loboplusia* is a very distinctive and unmistakable plusiine. In contrast, the female lacks all these features and has a similar appearance to an *Antoculeora*, although without its golden scaling.

I know of only five specimens of the sole species contained in *Loboplusia, L. vanderweelei* (Fig. 74); three males and two females. The holotype and paratype males were collected at 1700 m in west Java (Roepke, 1941). Subsequently, Dufay (1973) described two females as a separate species, *Autographa pokhara*. These were taken at 1500 m and 2000 m in Nepal and Burma respectively. The sexes were finally associated by Dierl (1975), who reported a third male, which he had taken in Nepal at 2360 m, near the locality of the holotype of *A. pokhara*. Little is known of the biology of the species, although Dierl (1975) stated that it is only to be found in very wet mountain forests receiving over 6000 mm of rain per year.

Clade 35 [113(0), *142(2), 198(1), 212(1),* 213(3)]. The three genera of clade 35, *Sclerogenia, Antoculeora* and *Autoplusia* are united by three good synapomorphies: the fusion of the saccular sheet with an overfold of the costa (142); increased sclerotization posterior to the ostium bursae (198); and differential sclerotization of the corpus bursae granulations (212). They also display strong sclerotized ridges on the apex of the corpus bursae (213), a feature also seen in *Macdunnoughia* (s.l.).

Sclerogenia [95(0), 108(1), 155(1)]. *Sclerogenia* is another monotypic genus. The sole species, *S. jessica* (Fig. 78), has several unique features of the genitalia not included in the current data set. The juxta has a very pronounced basal bulge, while the fused saccular sheet/costal overfold forms an elongate, ventrally curved process that just exceeds the bulged ventral edge of the valve (Fig. 361). The corpus bursae of the female is distinctive (Fig. 455) in that the apex is reflexed and fused along the posterior section of the fundus

and is entirely open to it internally, thus giving the appearance of two strigate ventral sacs. The remainder of the fundus is characteristically lemon-shaped.

Sclerogenia was initially erected as a subgenus of *Autographa* by Ichinosé (1973) to receive the species *jessica*, previously included in *Macdunnoughia* (Ichinosé, 1962*b*). Ichinosé (1973) still considered *S. jessica* to be closely related to *Macdunnoughia* (then also a subgenus of *Autographa*), in view of the similarities of the female genitalia. *Sclerogenia* was subsequently elevated to full generic status by Sugi (1982).

S. jessica is another species found in the eastern Palaearctic and southern Himalayan foothills. Hampson (1913) recorded the species from Japan, Assam and the Punjab, while it also occurs in China (Chou & Lu, 1978). There is also a single specimen in the BMNH collection from northern Luzon in the Philippines. The larva of *S. jessica* was described by Ichinosé (1960*a*). Its larval foodplants appear to be restricted to members of the Asteraceae: *Sonchus, Lactuca* (Ichinosé, 1973), *Ixeris* and *Arctium* (Miyata, 1983).

Clade 36 [158(0), *198(2), 199(1), 200(1)*]. *Antoculeora* is interpreted as the sister-group of *Autoplusia* on the basis of three synapomorphies: further sclerotization of the ventral area posterior to the ostium bursae (198); a ventral origin of the anterior apophyses (199); and a distinctive form of antrum (200). In addition, the aedeagus sclerotization of both genera is not restricted to a ventral band, instead the organ is generally sclerotized, as in the presumed plesiomorphic state.

Antoculeora [18(1), 104(1), 116(0), 117(0), *118(2)*, 145(1), 189(0), 191(1)]. The outstanding features of the genus *Antoculeora* are the highly modified and very distinctive genitalia. In the male, the whole of the genital capsule appears to have moved posteriorly and to have rotated somewhat dorsally. This has resulted in the pleurites losing contact with the dorsal edge of the tegumen arms, only retaining apical contacts (118), and straightening (116) and narrowing (117) in the process. The tegumen arms are extremely swollen anteriorly and, in dorsal view, diverge at 180 degrees (104), leaving a broad, U-shaped anterior emargination. The valves have become irregularly and strongly digitate, taking the form of a stag's antlers (Figs 376, 377). The tines are irregularly curved and asymmetrical, the left valve having three, the right four, so that they partially interlock when the valves are closed. The saccular sheet has become a long, apically serrate lance. The modifications in the female are less extreme but are doubtless partly correlated with those of the male. St7 is medially and posteriorly deeply emarginate, while the antrum has become a heavily sclerotized, open, irregularly and asymmetrically lobed chamber (Figs 436, 437, 456). Together, they form a unique genital complex within the Plusiinae.

There are three, perhaps four, very closely related species in *Antoculeora*: *A. ornatissima* (Fig. 79), *A. locuples, A. lushanensis* Chou & Lu and *A. minor* Chou & Lu, differing only in minor details of wing pattern and valve shape. They may all eventually be referable to a single species. Initially, *A. ornatissima* was placed by Kostrowicki (1961) in *Argyrogramma*. This, however, was based upon a misidentification (Ichinosé, 1963*a*; Dufay, 1970; Ichinosé, 1973). Ichinosé (1962*b*) included *ornatissima* tentatively in *Macdunnoughia*, then erected *Antoculeora* to accommodate it (Ichinosé, 1973). *Antoculeora* was first treated as a subgenus of *Erythroplusia* but a relationship with *Macdunnoughia* was also suggested (Ichinosé, 1973). This was formalized by Dufay (1977), who transferred *ornatissima* and *locuples* (as a synonym of the former) to *Macdunnoughia*. *Antoculeora* was resurrected as a full genus by Chou & Lu (1979*a*) and so treated by Sugi (1982).

A. ornatissima has a similar distribution to *Sclerogenia*: Japan, Korea, China, the far eastern U.S.S.R. (Primorskiy Kray), Sikkim, Punjab, Nepal and Bengal (Dufay, 1977). *A. minor* and *A. lushanensis* are so far only reported from China, while *A. locuples* is recorded in the BMNH collection from Japan and the U.S.S.R (Primorskiy Kray). Nothing is known about the biology of this genus. Ichinosé (1973) stated that the larvae had been reared on *Sonchus* and *Lactuca* but that the natural foodplant was unknown, while Miyata (1983) gave *Petasites*. If these prove correct, then *Antoculeora* displays the same oligophagy, restricted to the Asteraceae, as its close relative *Sclerogenia*.

Autoplusia [12(0), 14(2), 59(1), 64(1), 83(3), 131(0), 140(0), 216(1)]. *Autoplusia* is an exclusively New World genus that is in need of revision. Four species are currently recognized: *A. egena, A. olivacea, A. egenoides* Franclemont & Todd and *A. illustrata* (Guenée). To those can be added *'Syngrapha' gammoides* and I will limit my discussion to these five species. However, I understand from Mr F. Navarro that there are several more species, currently languishing in either *Syngrapha* or 'Plusia' (s.l.) that are assignable to *Autoplusia*.

A. egenoides was originally described by Hampson (1913) as the 'much darker' 'ab. 1' of *A. egena*. It was named 'ab. *egenoides*' by Strand (1917), a name employed subsequently by Draudt (1940). For some mysterious reason, it was elevated to full species by Franclemont & Todd (1983) in the latest North American checklist. Even the very inclusion of *A. egenoides* in that list is odd for, as far as I am aware, only

the holotype exists and that was collected in Mexico. Nevertheless, it would appear that *egenoides* has been wrongly associated from the outset. I have examined the holotype and conclude that *A. egenoides* is probably synonymous with *A. olivacea*. However, comparison of the genitalia is required to confirm this.

Autoplusia has a number of features in common with *Rachiplusia*, as noted above (characters 14, 64 and 216). It is also the only genus in the Plusiini to lack a saccular flange. In addition, as stated above, while the type species, *A. egena*, lacks a broad, triangular saccular spine (Fig. 372) (141), this structure is present in *A. olivacea* (Fig. 373) and *'Syngrapha' gammoides* (Fig. 374). The autoplusias also possess a number of genitalic synapomorphies. The saccular sheet/costal overfold fusion is extended into a curved hook, the apex of the valve forming an oval lobe arising from the external surface of this structure. The sacculus is extremely inflated. The everted vesica curves at about half its length through 90–200 degrees, the angle varying between individuals within a species. On the outer surface of the angle, there is a large, distally directed, thorn-like cornutus, while the apical half of the vesica is covered with numerous small, basally-directed cornuti, the arrangement of which is species specific. The distal part of the ductus bursae is heavily sclerotized, dorso-ventrally flattened and strigate, while the apex of the corpus bursae is elongated and apically recurved (Fig. 454). These features, with modifications, are present in *A. egena, A. olivacea* and *'Syngrapha' gammoides*.

A. illustrata, however, lacks all the valve apomorphies listed above but may have the thorn-like cornutus (Eichlin & Cunningham, 1978: fig. 59). The female genitalia also appear to share few features in common with the other members of the genus (Eichlin & Cunningham, 1978: fig. 95), while close examination of the forewing pattern reveals only a superficial similarity. *A. illustrata* was only tentatively included in the genus by Kimball (1965) and although Eichlin & Cunningham (1978) stated that the male genitalia supported this decision, I disagree. A detailed study of *Autoplusia* will probably show that *A. illustrata* (and the similar *'Syngrapha' egenella* (Herrich-Schäffer)) ought to be removed from this genus. At present, I cannot suggest a better placement.

'Syngrapha' gammoides (Figs 82, 83) is a Chilean endemic. Its life history and immature stages have been described in detail by Angulo (1973) and Angulo & Weigert (1975). It is recorded as feeding on several crop plants in Chile and is an economically important pest in that country. *A. egena* is found from the southern U.S.A. to Brazil and is also a pest species and high polyphagous (Eichlin & Cunningham, 1978). It is commonly known in the U.S.A. as the Bean Leaf Skeletonizer and there have been occasional serious outbreaks of this species (Kimball, 1965). The larvae have been described by Crumb (1956) and Eichlin & Cunningham (1978).

The last species, *A. olivacea* (Fig. 81), was stated by Eichlin & Cunningham (1978) to be found only in southern coastal California. However, in the course of this study, I found that there has been considerable confusion between this species and *A. egena* (Fig. 80). The most obvious wing pattern difference concerns the form of the terminal line between the forewing veins R_5 and M_3. In *A. egena*, it forms a distinct, single pink crescent (Fig. 80), while in *A. olivacea*, the terminal line in this section of the wing is less distinct and is broken into three small crescents, one between each pair of veins (Fig. 81). Additionally, in *A. egena*, the forewing postmedial line is a distinct, thin, brown line, which is flanked on its outer edge by a broader, pinkish brown band. It passes diagonally across the wing towards the apex but recurves basally just before it meets the costal margin (Fig. 80). In *A. olivacea*, only the pinkish brown band is present. This becomes very indistinct apically and does not recurve to meet the costa (Fig. 81). The Y-marks in both species are very variable and of no use in identification. Those illustrated in Figs 80, 81 represent extreme forms that occur in both species. These forewing pattern elements coincide with the much more distinctive genitalic differences (see Eichlin & Cunningham, 1978). From this discovery, I draw three conclusions. First, the specimens illustrated by Eichlin & Cunningham (1978: figs 168, 170) as *A. olivacea* and *A. egena* are both *A. olivacea*. Second, *A. olivacea* is much more widespread than was thought. Specimens in the BMNH collection have been taken in California, Mexico, Guatemala, Costa Rica and Colombia. Third, overall forewing ground colour is of little use in distinguishing the two species. While *A. olivacea*, when fresh, is distinctly darker and greener than *A. egena*, both fade to a similar pale brown. Incidentally, the holotype of *A. egenoides* has the forewing pattern of *A. olivacea*, hence my suggestion above that the two species may prove to be synonymous. The larva of *A. olivacea* has been described by Eichlin & Cunningham (1978) and, like *A. egena*, is polyphagous.

Clade 37: Plusiina [83(1), *146(1)*]. The constituent genera of the subtribe Plusiina are united solely by the apomorphic state of character 146, a blade-like valve. As already noted above (Characters), this character state is difficult to define but is readily recognized. The condition may have been misinterpreted in *Anagrapha* (q.v.).

Diachrysia [3(0), 9(1), 16(1), 58(0), *65(1)*, 165(1), 191(1)]. Ten species are currently placed in the Holarctic

genus *Diachrysia*. Two, *D. aereoides* and *D. balluca*, are Nearctic, the remainder Palaearctic, with a distinct concentration in Japan and neighbouring countries. As stated earlier, *Diachrysia* may not be monophyletic, particularly with regard to *Allagrapha*, and thus the sole autapomorphy included in the data set (65:1; the presence of a small number of large SD and D tarsal spines) may not be found much beyond *D. chryson* and *D. coreae* Ogata).

There appear to be three species-groups within *Diachrysia*. The *chryson* species-group comprises five species: *D. aereoides, D. leonina, D. bieti, D. chryson* (Fig. 84) and *D. coreae*. *D. aereoides* differs in being a small, paler brown moth than the others. It is widespread in the northern U.S.A. and southern Canada, extending south in the west to Colorado and in the east to Pennsylvania (Eichlin & Cunningham, 1978). The larvae are recorded as feeding upon *Mentha* (Lamiaceae), *Spiraea* (Rosaceae) (Crumb, 1956) and *Aster* (Forbes, 1954), and have been described by Crumb (1956) and Eichlin & Cunningham (1978). The other four species are among the largest plusiines and have somewhat falcate forewings. *D. bieti* and *D. leonina* are closely related and have brown forewings without any extensive metallic markings. The larva of *D. leonina* has been illustrated by Kogi (1986). It bears enlarged conical dorsal pinacula, very similar to those seen in the larva of *Anadevidia*. *D. leonina* is recorded as being polyphagous on such genera as *Urtica, Aster* and *Cirsium*. *D. coreae* is similar to *D. bieti* and *D. leonina* but bears a diffuse, subapical, quadrate, golden-green metallic patch on the forewing. It has long been regarded as synonymous with *D. chryson* (e.g. Kostrowicki, 1961), in which the patch is much more discrete and intense. Nothing is recorded of the biology of *D. coreae* but that of *D. chryson* is well known (e.g. Haggett, 1958; Bretherton *et al.*, 1983). The chaetotaxy has been described by Ichinosé (1962*b*). *D. chryson* appears to be facultatively monophagous on *Eupatorium* (Asteraceae) (e.g. Bretherton *et al.*, 1983) but other foodplants have been recorded: *Salvia, Mentha* (Lamiaceae) (Kostrowicki, 1961) and *Arctium* (Asteraceae) (Ichinosé, 1962*b*).

The *zosimi* species-group comprises only *D. zosimi*, and possibly *D. balluca*, although this latter species also shows some resemblances to the *chryson*-group. *D. zosimi* has a unique colour pattern, in which the forewings dorsal and distal of the discal cell are entirely metallic golden-green, with a 'crushed velvet' effect. The biology of this trans-Palaearctic species (Kostrowicki, 1961) has been described in detail by Kasy (1953). The larvae are polyphagous but mostly on species of Rosaceae (Kasy, 1953; Kogi, 1986). *D. balluca* has a similar forewing pattern to *D. zosimi* but has the large size and falcate forewing of the *chryson*-group. It is restricted to the north-eastern U.S.A. and south-eastern Canada. The larval chaetotaxy has been described by Eichlin & Cunningham (1978) and the foodplants have been given as *Humulus* (Cannabinaceae) (Saunders, 1873) and *Populus* (Eichlin & Cunningham, 1978).

The third species-group, exemplified by *D. chrysitis* (Fig. 85), comprises three species in which the forewing pattern consists of an H-shaped metallic patch, which may occasionally be represented by two separate, transverse bands instead. *D. stenochrysis* (Warren) has a more diffuse pattern than the other two, *D. chrysitis* and *D. nadeja*, and is restricted to the far eastern Palaearctic (Kostrowicki, 1961). The genitalia of *D. stenochrysis* can be difficult to distinguish from those of *D. chrysitis*, especially the males (Ronkay, 1982). *D. nadeja* was also thought to occur only east of the Ob' River basin, with isolated records as far west as Bessarabia (Kostrowicki, 1961). However, like *Macdunnoughia confusa, D. nadeja* appears to be undergoing a rapid westward expansion of range, having been recently discovered in Austria (Aistleitner & Rezbanyai, 1982), Switzerland (Rezbanyai, 1980) and France (Dufay, 1986). If this progression continues, then it may only be a matter of time before *D. nadeja* is captured in Great Britain and Scandinavia. The life history has been described by Rezbanyai (1983), with that of *D. chrysitis* for comparison. The natural foodplants of *D. nadeja* are unknown but *Urtica* and *Plantago* (Plantaginaceae) were accepted in captivity (Rezbanyai, 1983).

D. chrysitis is a very variable species, as evidenced by no fewer than 14 varietal and aberrational names. The species is widespread across the Palaearctic from Ireland to Japan. The immature stages have been described in detail by Rezbanyai (1983) and numerous other accounts exist (e.g. Bretherton *et al.*, 1983). The main larval foodplant is *Urtica* but many other species can be utilized.

There is also an occasionally recurrent taxonomic problem concerning *D. chrysitis* and the supposed species *D. tutti* (Kostrowicki). *D. tutti* was described as a separate species from *D. chrysitis* (Kostrowicki, 1961) on the basis of smaller size and minor differences in forewing pattern and in the genitalia (Bretherton *et al.*, 1983). Lempke (1965) examined a long series of Dutch specimens and agreed that tnere were two species, although there was also a great deal of intraspecific variation. However, Lempke (1966*a*) subsequently re-examined some of his material and found that, with the aid of two pins, he could transform the narrow ostium bursae [= antrum] of *D. chrysitis* into the broader ostium bursae of *D. tutti*. He thus concluded that he had been wrong and that there was, after all, only one species, *D. chrysitis*, which was subject to geographic variation (not unexpected given the extensive range of the species). Bretherton *et al.* (1983) regarded *tutti* merely as an aberration of *D. chrysitis*. However, Rezbanyai (1985) has recently

suggested that *tutti* may represent an eastern subspecies of *D. chrysitis* that is only partially reproductively isolated from the nominate subspecies by incomplete pheromonal differences. The two taxa, which have subsequently become partially sympatric, are thus currently in the process of hybridizing, further clouding the distinction between them. The problem is obviously not yet fully resolved.

Clade 38 [105(1)]. This clade is supported by only a very homoplasious character state and is unlikely to be corroborated by the results of future analyses.

Anagrapha [64(2), 113(1), 127(2), 143(2), 144(1), 189(1)]. *Anagrapha* is yet another of those genera that shares putative synapomorphies with two widely separated groups of genera on the cladogram. The genus is usually associated with *Syngrapha* (s.l.), due to the spined hind tibiae (64) and certain larval characters (see below). They also share a juxta with a subapical process (127) and a T8 that is irregularly cut back ventral to the base of the anterior apophysis (189). However, this latter character state also occurs in the Autoplusiina, while a broad, flat, cone-like vinculum (113) further supports a relationship between some members of this tribe and *Anagrapha*. Lastly, there is a remarkable similarity between *Anagrapha* and *Macdunnoughia* (s.str.) (especially *M. confusa*) in forewing pattern (cf. Figs 86, 76 respectively).

However, *Anagrapha* shows none of the genitalic features characteristic of *Macdunnoughia* and its relatives, although it has a number of autapomorphies. The harpe is bulbous basally and apically, and is bent outwards at 90 degrees at about half its length. The valve is deeply excavated apically and the costa has a fringe of dense, persistent, yellow hair. The costa terminates in a single distinct spine while the distal part of the sacculus bears broad, curved setae, somewhat like those found in *Ctenoplusia* and its relatives. In the female, the apex of the corpus bursae is recurved, as in many autoplusiines, but, while heavily sclerotized, lacks the characteristic strong internal ridges of that subtribe (Fig. 459).

Anagrapha was erected by McDunnough (1944) to accommodate the species *A. falcifera* (Fig. 86). With its markedly different genitalia, the species was considered to be a highly divergent branch of *Syngrapha*. Eichlin & Cunningham (1978) agreed with this interpretation and synonymized *Anagrapha* with *Syngrapha*, tentatively deriving *A. falcifera* from the *Syngrapha diasema* lineage. One of the main reasons for their placing of *Anagrapha* was the presence of seta SV2 on segment A1 of the larva. The feature was used to unite *Syngrapha, Anagrapha, Plusia* and a branch of *Autographa*. However, while this seta also occurs in *Sclerogenia* and *Macdunnoughia* (s.str.) (Ichinosé, 1962*b*), tantalizingly, it is absent in all other members of the Autoplusiina known so far, and most notably in *Puriplusia* and *Allagrapha*. Thus, the relationships of *Anagrapha* are as problematical using larval characters as with using adult characters and they are still far from clear. *Anagrapha* was subsequently reinstated to full generic status by Franclemont & Todd (1983).

A. falcifera is an abundant species throughout the U.S.A. and southern Canada (Eichlin & Cunningham, 1978). No records are known for the countries south of the U.S.A. Commonly known as the Celery Looper, the larvae sometimes cause economic losses to crops (Forbes, 1954). Overall, however, *A. falcifera* appears to be of only minor agricultural importance.

Clade 39 [12(1), 108(1), 109(1)]. The most characteristic feature of clade 39 is the strongly S-shaped vinculum, when seen in lateral view. However, this state is also weakly expressed in clade 21 of the Euchalciina and further evidence is required to support the monophyly of clade 39.

Autographa gamma [18(0)]. *Autographa gamma* (Fig. 87) was chosen to represent that branch of the genus characterized by the lack of seta SV2 on segment A1 of the larva (Eichlin & Cunningham, 1978). It is thus part of an overtly paraphyletic group of uncertain limits (cf. *Trichoplusia*). Eichlin & Cunningham included ten species of *Autographa* in this group, divided into three lineages, depending upon the number of processes on the ribs of the larval mandible.

The first lineage, *A. precationis* (Guenée) and *A. bimaculata* Stephens, was interpreted as the most primitive because the processes on both ribs 2 and 3 had been retained. McDunnough (1944) noted that *A. precationis* was unusual and displayed a number of features in common with the Argyrogrammatini, notably a bulbous coecum (157) and apical, basally-directed, setose scales on the valve (136).

The next most derived lineage had lost the process on the third mandibular rib and also comprised two species, *A. sansoni* and *A. rubida* Ottolengui.

Those species that had lost both mandibular processes were considered to be the most derived and included six Nearctic species: *A. biloba, A. californica, A. pseudogamma* (Grote), *A. v-alba* Ottolengui, *A. pasiphaeia* (Grote) and *A. flagellum* (Walker). However, Neil (1984) has shown that the larva of *A. flagellum*, which was unknown to Eichlin & Cunningham (1978), does possess a process on mandibular rib 2, and thus may be more closely related to *A. sansoni* and *A. rubida*.

Of the Palaearctic species, five were examined from specimens in the BMNH collection, of which *A. gamma* was found to lack SV2 on A1 (so too did *A. bractea*, see below).

Of the species for which life histories have been elucidated, most have been shown to be polyphagous on herbaceous plants. A few (*A. bimaculata, A. pasiphaeia, A. flagellum*) have been recorded from only one or two genera of larval foodplants (Eichlin & Cunningham, 1978), but this may reflect lack of information rather than true oligophagy.

Two species are serious agricultural pests; *A. gamma* in the Palaearctic (Carter, 1984 and references therein) and *A. californica* in the western Nearctic (Hyslop, 1912). *A. biloba* is an occasional pest of garden crops (Forbes, 1954).

Clade 40 [6(0), 215(1)]. The members of clade 40 are united by the synapomorphic possession of a lateral patch of thickened membrane on the corpus bursae (215). This feature is, however, lost in clade 44 (*Syngrapha* s.l.) and this must weaken the expectation that clade 40 will be corroborated by future studies.

Clade 41 [*215(2)*]. *Autographa bractea* and *Cornutiplusia* are united as sister-taxa by the further development of the lateral thickened membrane on the corpus bursae into at least a shallow pouch (215). This structure also occurs in the presumed close relatives of *A. bractea* (see below), *A. aemula* and *A. excelsa* (Kretschmar) (Kostrowicki, 1961).

Autographa bractea [6(0), 12(0)]. *A. bractea* (Fig. 88) was originally chosen to represent the second *Autographa* lineage comprising species that possess seta SV2 on larval segment A1. The choice was made by picking the British equivalent of an American species (*A. metallica* (Grote)) included in the second lineage by Eichlin & Cunningham (1978). However, they had not examined the larva of *A. metallica* and when, subsequent to my decision, I examined the larva of *A. bractea*, I found that it actually *lacked* seta SV2 on A1. *A. bractea* (and presumably those species, including *A. metallica*, that share the distinctive forewing pattern; see below) is thus referable to the presumed plesiomorphic (paraphyletic) lineage of *Autographa* exemplified by *A. gamma*. I will therefore discuss two further subgroups of *Autographa, A. bractea* and its relatives, and those species *known* to possess seta SV2 on A1.

A. bractea could be considered to be part of a species-group in which the Y-mark has become modified into an enlarged, single, silver or gold spangle. There are five species with such a pattern: *A. bractea, A. metallica, A. aemula, A. excelsa* and *A. kostjuki* Kljutshko. The group is Holarctic in distribution, although *A. metallica* is the only American representative. The life histories of three are known: *A. aemula* (Hirschke, 1898), *A. excelsa* (Laasonen & Skvortsov, 1984) and *A. bractea* (e.g. Beck, 1960; Bretherton *et al.*, 1983). All three species are polyphagous but with a preference for the Asteraceae.

There are six species currently placed in *Autographa* that are known to have seta SV2 on segment A1: *A. corusca, A. mappa, A. ampla* (Eichlin & Cunningham, 1978), *A. nigrisigna* (Walker) (Ichinosé, 1958*a, b*), *A. jota* and *A. pulchrina* (Kitching, unpubl. data). The first three appear to feed as larvae primarily on woody plants (Eichlin & Cunningham, 1978), although only *A. ampla* may be adequately recorded. While the other three are polyphagous on herbaceous plants (Beck, 1960; South, 1961; Miyata, 1983), *A. jota* will also feed on unspecified deciduous trees and shrubs (Bretherton *et al.*, 1983). *A. nigrisigna* is an agricultural pest in the eastern Palaearctic, where it is known as the Asiatic Common Looper or the Cabbage Semilooper. There have been numerous studies of its bionomics (Ichinosé, 1959; 1960*b*; Ichinosé & Asawa, 1964; Ichinosé & Shibuya, 1959), while the chaetotaxy of the larva must be the most over-described of any plusiine, this having been presented in detail in at least three separate papers (Mukerji & Singh, 1951; Ichinosé, 1960*a*; Betala & Kushwaha, 1972).

As was noted for *Thysanoplusia*, delimiting a group based on larval characters, when the larvae of only a few species are known, results in many species possibly being wrongly excluded. There are several autographas that fall into this category, and the elucidation of their life histories is an important prerequisite to a comprehensive revision of the genus.

Cornutiplusia [64(1), *215(3)*]. In *Cornutiplusia*, the lateral pouch of the corpus bursae mentioned above (clade 41) is produced into a large pouch or into an appendix. The degree of development of this structure is geographically variable and is the subject of another study (Kitching, in prep.). *Cornutiplusia* also has spined hind tibiae and was thus associated with the genus *Syngrapha* (Hampson, 1913). Kostrowicki (1961), however, thought the general appearance and genitalia suggested a closer link with *Autographa*. *Cornutiplusia* **stat. rev.** is here treated as a good genus, certainly distinct from *Syngrapha*, perhaps less so from *Autographa* (s.l.).

Cornutiplusia comprises a single species, *C. circumflexa* (Fig. 89), found throughout the more arid areas of southern Europe, North Africa and western Asia, as far as Sri Lanka and Lake Balkhash (U.S.S.R.).

The species extends down the African rift valley to Kenya and Uganda, and there are isolated populations on Grand Comoro and in South Africa/Namibia and the Gambia. The life history and larva have only been very briefly described (Kirby, 1907). The larval foodplants have generally been stated to be members of the Solanaceae (Kirby, 1907; Kostrowicki, 1961; Pinhey, 1975, who also gave *Eschscholzia* [Papaveraceae]).

Clade 42 [166(1)]. The three taxa that constitute clade 42 (*Plusia, Lophoplusia* and *Syngrapha* (s.l.)) are united by their apparent shared possession of a grooved subapical cornutus. However, as discussed above (648-step cladograms), the presence of such a structure has yet to be confirmed in *Syngrapha* (s.l.). The species examined in this study all lacked a true subapical cornutus and were coded 'not comparable'. The results of future studies may therefore show that character 166 is actually a synapomorphy for *Plusia* and *Lophoplusia*.

Plusia [12(0), 58(0), 83(3), 105(0)]. *Plusia* is a small genus containing at least five good species and a number of other dubiously distinct taxa. All except one (*P. venusta* Walker) have a diagnostic forewing pattern consisting of a yellow to deep orange ground colour, with the Y-mark modified into two large, silver spangles and a white dash present in the cell M_1, between the discal cell and the subterminal line (Fig. 90). In *P. contexta* Grote, these markings have become somewhat elongate, a transformation series that culminates in *P. venusta* (Fig. 91). In this species, the Y-mark has become a thin, white streak, while the ground colour of the forewing has become pale brown with cream margins. It thus superficially resembles other noctuid genera such as *Mythimna* Ochsenheimer and *Simyra* Ochsenheimer. All species of *Plusia* also have reduced dorsal abdominal tufting.

The species are all very similar in their genitalia. The males of *P. venusta, P. putnami* Grote and *P. nichollae* (Hampson) cannot be reliably distinguished, while the females of the first two are similarly virtually identical. *P. festucae* differs from *P. putnami* on minor points of genitalic structure, such as having a larger clavus, a longer subapical cornutus that is pointed at both ends and a shorter ductus bursae (Lempke, 1966*b*; 1969; Dufay, 1969; Bretherton *et al.*, 1983). The males of *P. contexta* are unique in that the valve costa terminates in a narrow, blunt projection (Eichlin & Cunningham, 1978). *P. festucae* and *P. nichollae* differ from the other three species in having a somewhat round sclerotization on the corpus bursae rather than one that is elongate.

The genus *Plusia* is Holarctic. *P. festucae* (Fig. 90) occurs across the Palaearctic region from the British Isles to Japan. It is highly variable in size and wing pattern and this has led to the naming of numerous aberrations, varieties and parochial subspecies of doubtful reality. *P. putnami* is even more widespread and has a similar number of subspecific and infrasubspecific names. Four subspecies are currently recognized: *P. p. putnami* occurs west across the northern U.S.A. and southern Canada to the Rocky Mountains but is absent from the central states (cf. *Pseudeva purpurigera*) (Eichlin & Cunningham, 1978); *P. p. gracilis* (Lempke) is restricted to western Europe (Dufay, 1969; Bretherton *et al.*, 1983); *P. p. barbara* (Warren) is known only from a unique female holotype from Morocco; and *P. p. festata* Graeser occurs in the eastern Palaearctic, from the Ob' River basin to Japan. The remaining three species are all North American. *P. venusta* and *P. contexta* have similar ranges to *P. p. putnami*, although neither extends as far west, while *P. nichollae* is restricted to the west coast, from northern California to southern Alaska.

Larval foodplants are known for all species except *P. nichollae*. The genus *Plusia* feeds primarily on grasses, sedges and other marsh and waterside monocotyledons (Beck, 1960; Dufay, 1969; Eichlin & Cunningham, 1978; Bretherton *et al.*, 1983; Miyata, 1983). The last group includes *Sparganium* (Sparganiaceae), *Typha* (Typhaceae), *Iris* (Iridaceae), *Alisma* (Alismataceae) and *Juncus* (Juncaceae). *P. festucae* has also been reared on *Crocosmia* (Iridaceae), *Salix, Brassica* and *Linum* but these are species accepted in captivity, rather than the natural foodplants. The larva shows several features unique in the Plusiinae that are probably linked to its monocotyledonous diet. It is elongate, slender and cylindrical (Bretherton *et al.*, 1983) and the head is about as wide as the rest of the body. The larva does not, therefore, taper anteriorly as is typical of other plusiines. The crotchets are uniordinal, while the mandibles have a deep pocket on the inner ventral edge that is apparently a modification for feeding on grasses (Eichlin & Cunningham, 1978). Pupation occurs in an elongate, strong, white cocoon, spun vertically on the underside of the leaves of its foodplant and is placed near the apex so as to cause the leaf tip to droop and conceal it (South, 1961).

Clade 43 [59(0), 144(1), *166(2)*]. There are no convincing synapomorphies at present to unite *Lophoplusia* and *Syngrapha* (s.l.) as sister-groups. Characters 59 and 144 have been shown to be highly unreliable. The possibility that a grooved or winged subapical cornutus (166) actually represents a synapomorphy for *Lophoplusia* and *Plusia*, to the exclusion of *Syngrapha* (s.l.), has been discussed above.

Lophoplusia [18(0), *46(2), 47(1),* 65(3), 107(1), 144(2)]. The genus *Lophoplusia* is endemic to the

Hawaiian Islands. There are currently four described species: *L. pterylota* (Fig. 92), *L. psectrocera*, *L. violacea* (Swezey) and *L. giffardi* (Swezey), with a possible fifth undescribed species represented in the BMNH collection. The most readily recognizable feature of all species is the bipectinate antennae of both sexes (46, 47) and this was the character state used by Zimmerman (1958) to define *Lophoplusia* when first described. In addition, *L. pterylota* has numerous long, fine SD and D tarsal setae (65) and a single, dorsal bar on the anal tube (107). *L. giffardi* shares the distinctively winged subapical cornutus (Zimmerman, 1958: fig. 303) but its presence in the other species requires confirmation.

Little is known about the biology of *Lophoplusia*. *L. violacea* and *L. pterylota* have recently been reared on *Stenogyne* (Lamiaceae) and *Clermontia* (Lobeliaceae) respectively (K. Sattler, pers. comm.).

Clade 44: *Syngrapha* (s.l.) [64(1), 97(1), 127(2), 149(1), 162(0), 189(1), 191(1), 201(1), 215(0)]. *Syngrapha* (s.l.) (i.e. including *Palaeographa* and *Caloplusia*, but excluding *Cornutiplusia* and *Anagrapha*) is a large genus of about 35 species. Its members are generally characterized by spined hind (and occasionally other) tibiae but this character state also occurs in several other plusiine taxa, particularly if occasional spines are counted (see Character analysis). The three taxa examined in this study also shared several other features of interest. They are the only members of the Plusiini to have a straight uncus (97) and a sclerotized, sharply pointed, hook-like harpe (149). Like *Anagrapha*, they have a subapical juxtal process (127) and a T8 cut back ventrally below the base of the anterior apophysis (189). This feature also occurs in the Autoplusiina (clade 30).

On Eichlin & Cunningham's (1978) phylogenetic tree, *Syngrapha* occupied the apex, as the sister-group of *Plusia*. They recognized a maximum of ten lineages within *Syngrapha* (excluding *Anagrapha*). I will discuss four of these in this section, following the topology of Eichlin & Cunningham's tree. *S. surena* (Grote) will be discussed under *Palaeographa*; the *celsa* and *rectangula* species-groups under clade 45; and *Palaeographa, Syngrapha* (s.str.) and *Caloplusia* in their own sections. More detailed descriptions of the Nearctic species are given by McDunnough (1944) and Eichlin & Cunningham (1978).

S. ottolenguii was considered by Eichlin & Cunningham to be the most primitive *Syngrapha*. In many ways, the species is halfway between this genus and *Autographa*. *S. ottolenguii* has the elongate, heavily sclerotized antrum, the ventral edge of which projects beyond the ostium bursae (191; a feature seen in *Palaeographa* and *Caloplusia* but not in any *Autographa*) and also spined hind tibiae (Eichlin & Cunningham, 1978). However, the male genitalia are very similar to those of many *Autographa* species, especially in having a long clavus (all other syngraphas have reduced clavi). Given that the form of the female genitalia is likely to be apomorphic, while that of the male plesiomorphic, I will retain *ottolenguii* in *Syngrapha*. McDunnough (1944) and Franclemont & Todd (1983) took a different view and placed the species in *Autographa*. Either way, *S. ottolenguii* is clearly another 'critical species' and knowledge of its immature stages is imperative. The species is restricted to Alaska and the Yukon Territory, west of the Mackenzie River (Eichlin & Cunningham, 1978).

The next group proposed by Eichlin & Cunningham was a paraphyletic assemblage of all the remaining syngraphas that lacked seta SV2 on larval segments TII and TIII. Three lineages (excluding *Anagrapha*) were recognized within this group. The most primitive, in that its members retained the raduloid on the larval hypopharynx, comprised four species: *S. selecta* (Walker), *S. epigaea, S. altera* (Ottolengui) and *S. octoscripta* (Grote). The larvae of *S. epigaea* and *S. selecta* have been described by Eichlin & Cunningham (1978). The former appears to be highly polyphagous on various trees and shrubs, while records for *S. selecta* require confirmation due to confusion with the superficially very similar *S. viridisigma* (q.v.). Like that species, *S. selecta* may also be shown to be restricted to conifers. *S. octoscripta* has been recorded as feeding on *Vaccinium*. This group of syngraphas occurs across the northern U.S.A. and southern Canada. *S. altera* is restricted to east of the Great Lakes; *S. epigaea* extends southward into Oregon, Wyoming and Colorado; *S. octoscripta* ranges farther north to Alaska and Newfoundland; while *S. selecta* is so far known reliably from scattered localities (Eichlin & Cunningham, 1978).

Of those species that lack both SV2 and TII and TIII and a raduloid, *S. viridisigma* was considered the most primitive, due to genitalic and wing pattern similarities with the *selecta* species-group. As stated above, this species is frequently confused with the rarer *S. selecta* but the genitalia of the two species are distinct. The larva was described by Eichlin & Cunningham (1978) and various conifers were listed as larval foodplants. Some of these may, however, refer to *S. selecta*. *S. viridisigma* occurs throughout Canada, and is found also in the far north-eastern U.S.A. and in the Rocky Mountains as far south as New Mexico.

The most advanced group of syngraphas lacking seta SV2 on TII and TIII (excluding *Anagrapha*) was considered to be the *diasema* species-group. All these species have pale yellow hindwings, similarly patterned forewings and show similarities in genitalic structure (Eichlin & Cunningham, 1978). The included species were: *S. diasema, S. snowii, S. sackenii, S. borea, S. diversigna* and *S. orophila*. The larval foodplants of only two species are known; *Vaccinium* (*S. orophila*; Crumb, 1956) and *Betula* and *Populus*

(*S. diasema*; Kostrowicki, 1961). *S. diasema* occurs throughout central Canada and southern Alaska (Eichlin & Cunningham, 1978), and is also found in Scandinavia and the north-eastern U.S.S.R. It is probably circumpolar in distribution (Kostrowicki, 1961). *S. snowii* is apparently endemic to New Mexico, while *S. borea* is found in the far north of Canada and in Greenland. *S. diversigna* occurs in the Canadian Rockies and southern Alaska, and is broadly sympatric with *S. orophila*, which extends further south to Wyoming. *S. sackenii* is found on the eastern slopes of the Rocky Mountains in the U.S.A. and Alberta, and appears to be sympatric with *S. orophila* in that part of the latter's range in which *S. diversigna* is absent (Eichlin & Cunningham, 1978).

Palaeographa [6(1)]. When *Palaeographa* was first described as a subgenus of *Syngrapha* (Kljutshko, 1983), four species were included: *S. interrogationis, S. alpina* Ichinosé, *S. gilarovi* Kljutshko and *S. transbaikalensis* (Staudinger). *S. alpina* had previously been synonymized with *S. nyiwonis* Matsumura (Sugi, 1982), and this latter taxon is also referable to *Palaeographa*. Other candidates include *S. pyrenaica* Hampson, *S. flammifera* Chou & Lu and *S. u-aureum* (Guenée). These last three species have all, at one time or another, been considered synonyms of *S. interrogationis*. *S. transbaikalensis* apparently grades into *S. interrogationis* in Korea (Ronkay, 1982) and may thus be yet another form of the latter.

As for the previous major *Syngrapha* subgroup, those species that possess seta SV2 on segments TII and TIII were also subdivided by Eichlin & Cunningham (1978) based upon the presence or absence of the raduloid. *S. interrogationis* and *S. u-aureum* (together with *S. surena*, see below) constituted that lineage in which the raduloid was retained and was therefore considered primitive. This taxon may correspond to *Palaeographa* but confirmation of the presence of the raduloid in the larvae of the other species is required. Also, at present, well-documented synapomorphies for the members of *Palaeographa* are needed to corroborate the monophyly of the subgenus.

S. interrogationis (Fig. 93) is a widespread Holarctic species. It occurs in northern Canada and Alaska (Eichlin & Cunningham, 1978), throughout northern and western Europe (the British Isles, Iceland, Scandinavia) and east through central U.S.S.R. to the Pacific seaboard. *S. pyrenaica* is endemic to the Pyrenees and may be no more than a local race of *S. interrogationis*. *S. transbaikalensis*, as its name suggests, occurs in the north-eastern Palaearctic region, east of Lake Baikal to Japan and Kamtchatka. *S. nyiwonis* is found in Japan and the neighbouring land areas of Sakhalin and the Kurile Islands (Ichinosé, 1963*b*). Further details of the distribution and ecology of '*S. alpina*' were provided by Kljutshko (1983), who also stated that *S. gilarovi* was restricted to the area of Kamtchatka. *S. flammifera* was described as an aberration of *S. interrogationis* by Hoyningen-Heune (1901) but was subsequently elevated to full species level, from subspecies (sic), by Chou & Lu (1979*b*). Given that the collection locality of the original specimen of *flammifera* was Estonia and Chou & Lu presumably examined specimen(s) from China, then either *S. flammifera* is a very widespread (or disjunct) but rare and highly undercollected species or, as is generally considered, is merely a form of *S. interrogationis*. The diagnostic characters used by Chou & Lu (1979*b*) ('transverse cordate stigma of [the] fore-wing and [the] truncate apex of the clavus') suggest that the latter hypothesis is most likely correct. *S. u-aureum* occurs throughout Canada and the north-eastern U.S.A., with an isolated record from Colorado (Eichlin & Cunningham, 1978).

The life history of only one species is known, European *S. interrogationis* (Bretherton *et al.*, 1983). These authors give *Calluna* and *Vaccinium* (Ericaceae) as larval foodplants, while Kostrowicki (1961) added *Erica* and *Urtica*. *S. u-aureum* is said to feed on *Vaccinium* (Forbes, 1954) but no further details of its biology are known.

A second species, *S. surena*, was associated with *S. interrogationis* by Eichlin & Cunningham (1978) on the basis of similar genitalia. *S. surena* is very rare, Hampson (1913) never saw it and Eichlin & Cunningham (1978) knew of less than a dozen specimens. It occurs in Newfoundland, Ontario, Quebec and Maine.

Clade 45 [7(1), 24(1), *127(3)*]. Three synapomorphic character states unite *Syngrapha* (s.str.) and *Caloplusia* as sister-groups. All members of both taxa (see below) have yellow hindwings (7) except *S. parilis*, in which they are white. A juxta with a subapical, sharp spine (127) is also almost universal but is absent in *S. montana*. Small eyes with a prominent rim (24) are restricted to a subset of potential members of clade 45; *Caloplusia, Syngrapha devergens* and *S. ignea*. All three of these conditions are absent in the putatively related *celsa* and *rectangula* species-groups, which I will now discuss, separately from *Syngrapha* (s.str.) and *Caloplusia*.

Eichlin & Cunningham (1978) considered as most highly evolved, that branch of *Syngrapha* in which seta SV2 was present on segments TII and TIII of the larva but the raduloid had been lost. Four lineages were recognized within this group. *Caloplusia* (q.v.), with spines on all the tibiae, was interpreted as the first lineage to diverge. Next was the *rectangula* species-group, which was considered to be closely related based

on similarities in larval and genitalic structure. The *celsa* species-group formed the sister-group of *Syngrapha* (s.str.). Thus clade 45 was treated by Eichlin & Cunningham (1978) as polyphyletic (Farris, 1974), and the three synapomorphies listed above would have to be interpreted as convergent developments. Further study of *Syngrapha* is required to clarify this issue.

The *celsa* species-group comprises only *S. celsa* and *S. angulidens*. Both species feed as larvae on various conifers (Crumb, 1956; Ross & Evans, 1957; Prentice, 1962). Nothing further is known of the biology of *S. angulidens* but the larva of *S. celsa* was described by Crumb (1956) and Eichlin & Cunningham (1978). *S. celsa* is restricted to the western slopes of the Rocky Mountains from Alaska to southern California, while *S. angulidens* is found on the eastern slopes, from southern Canada to Arizona. There are also records of *S. angulidens* from New Hampshire and Nova Scotia in the east (Eichlin & Cunningham, 1978).

The *rectangula* species-group comprises four species: *S. rectangula, S. alias* (Ottolengui), *S. abstrusa* Eichlin & Cunningham and *S. cryptica* Eichlin & Cunningham. The latter two species have only recently been separated from *S. alias* (Eichlin & Cunningham, 1978). Nothing is known about their biology but some of the records reported for *S. alias* may well apply to these species. Like the *celsa*-group, *S. rectangula* and *S. alias* feed as larvae on diverse species of conifers (Crumb, 1956; Ross & Evans, 1957; Prentice, 1962; Tietz, 1972). This habit was, together with the presence of SV2 on TII and TIII, sufficient for Crumb (1956) to consider proposing a separate genus (genus no. 11). However, the setal character is now known to be much more widespread and so only monophagy on conifers remains as a putative synapomorphy for the *rectangula* and *celsa* species-groups. *S. alias* and *S. rectangula* are found across the northern U.S.A. and southern Canada, although the former also extends along the Rocky Mountains north to the Yukon Territory and south to Arizona. The distributions of the other two species are likely to be incomplete, due to confusion with *S. alias*. *S. cryptica* has so far been recorded from Wisconsin, Michigan and New Hampshire, and *S. abstrusa* additionally from Ontario and Maine (Eichlin & Cunningham, 1978).

Syngrapha* (s.str.)** [83(0)]/Caloplusia*** [59(1), *63(2)*, 64(2)]. I will deal with these two taxa together because the distinction between them has been blurred in recent years. *Caloplusia* was originally erected by Smith (1884) for those northern species of 'Plusia' (s.l.) with ovate eyes and spines on all the tibiae. However, there were no explicitly included species until *C. hochenwarthi* and '*C. devergens*' were placed in the genus some seven years later (Smith, 1891). Warren (1913) designated *C. hochenwarthi* as type species in April 1913 (Nye, 1975) and added *C. tibetana* (Staudinger) and *C. composita* Warren. Hampson (1913; November) subsequently employed the same type species and added '*C. virgula*' (now *Rachiplusia*), *C. alticola* (Walker) and *C. ignea* (Grote). In both works, *Caloplusia* was distinguished from *Syngrapha* by the possession of spines on all the tibiae, rather than on just the hind tibiae (characters 63 and 64). Both authors also incorrectly cited *Syngrapha ain* (Hochenwarth) as the type species of that genus and thus *S. devergens* could be comfortably accommodated in *Caloplusia*.

This error was corrected by McDunnough (1944) and *devergens* (together with *alticola*) was transferred to *Syngrapha*. McDunnough's discovery that neither of these two species had the extensive tibial spining claimed for them (an observation confirmed in the present study) allowed him to leave *Caloplusia* as a distinct genus. The separation was retained by Forbes (1954), Crumb (1956) and Kostrowicki (1961). The last author committed the same error as Hampson (1913) but on this occasion it was *S. interrogationis* that was mistakenly treated as the type species of *Syngrapha*.

Eichlin & Cunningham (1978) held the opinion that the degree of tibial spining was not a character of genus-level significance and synonymized *Caloplusia* with *Syngrapha*. However, only *ignea* was explicitly transferred; *hochenwarthi* was included only by default. Franclemont & Todd (1983) followed this synonymy and also sank the Nearctic *S. alticola* to the Palaearctic *S. devergens*.

There are thus eight species in clade 45 as constituted in this study. For convenience, I shall retain the names *Caloplusia* and *Syngrapha* (s.str.). The latter includes *S. devergens* (Fig. 94), *S. montana, S. microgamma, S. parilis* (Fig. 96) (following Eichlin & Cunningham, 1978) and *S. ain*. The last species has never previously had its relationships within *Syngrapha* analysed. An examination of the male genitalia of *S. ain* figured by Ichinosé (1962*b*) showed that it has the same general facies and large, basal, strongly curved cornutus on the vesica as *S. microgamma*, and it would seem that the two may be sister-species. *Caloplusia* comprises *C. hochenwarthi* (Fig. 95), *C. composita* and *C. ignea*.

The biology of none of the Nearctic species of *Caloplusia* or *Syngrapha* (s.str.) is known, nor of the Nearctic populations of the Holarctic species. In Europe, *S. ain* is recorded as feeding as a larva on *Larix* (Pinaceae); *S. microgamma* on *Salix* (Salicaceae); *S. devergens* on *Silene* (Caryophyllaceae), *Viola* (Violaceae), *Plantago* (Plantaginaceae) and *Geum* (Rosaceae); and *C. hochenwarthi* on various umbellifers (Kostrowicki, 1961). Tietz (1972) added numerous arctic-alpine plants to the list for *C. hochenwarthi* (*Antennaria, Carex, Castilleja, Gentiana, Penstemon, Salix* and *Vaccinium*). The larva of *C. hochenwarthi* has been briefly described by Kirby (1889), but the chaetotaxy of all the species remains virtually unknown.

A larva of *S. ain* examined in the course of this study proved to possess seta SV2 on segments TII and TIII.

S. montana is the only wholly Nearctic species of *Syngrapha* (s.str.). It occurs mostly in the north-eastern corner of the U.S.A. and adjacent areas of Canada south of the St Lawrence river. There are isolated records from Wisconsin and Saskatchewan. The other endemic Nearctic species is *Caloplusia ignea*, found mainly in the Rocky Mountains from Alaska to California and Colorado, with additional records across northern Canada (Eichlin & Cunningham, 1978). *C. composita* is known only from the mountains south-east of Lake Balkhash (U.S.S.R.), while *C. hochenwarthi* has a disjunct distribution in Scandinavia, the European Alps, Macedonia, and various localities throughout the U.S.S.R. from Armenia and the Caucasus to the Amur river and Kamtchatka (Kostrowicki, 1961). *Syngrapha ain* occurs in the mountains of central Europe and in the central U.S.S.R. from Lake Balkhash to the River Lena. There are also records from the Amur river (Kostrowicki, 1961).

The remaining three species are Holarctic. *S. microgamma* is present throughout central Europe, Scandinavia and along the Baltic coastline, with scattered records in the central U.S.S.R. and Kamtchatka, and throughout Canada and the northern U.S.A., with an isolated record from Colorado. *S. devergens* also occurs in the European Alps, Scandinavia and south-east of Lake Balkhash and in the Nearctic, extends throughout the Rocky Mountains from Alaska to Colorado, and across to Hudson Bay. *S. parilis* is circumpolar at high latitudes in Canada, Alaska, Greenland, Scandinavia, the Arctic Ocean coasts and Novaja Zemlya (U.S.S.R.) (Eichlin & Cunningham, 1978; Kostrowicki, 1961). Its absence from localities further east is almost certainly due to lack of collecting in these areas.

Intra-outgroup analysis

The cladistic relationships between the outgroup taxa are not of primary importance in this study. However, several interesting patterns were found and it might be useful, for future studies, to discuss them briefly. I will only deal with six of the possible ten outgroup clades.

The complement of clade 51 [38(0), 40(0), 48(1), *56(1)*, 178(1)]. If the cladogram shown in Fig. 27 is rerooted on the branch subtending clade 51, then a new clade is formed (the complement of 51) that hypothesises that the sister-group of the plusiines is clade 47 (*Magusa* + the stictopterines + the euteliines). As might be expected, given that this topology is only one of several possible (see 648-step cladograms), the data supporting this sister-group relationship are relatively weak. The Plusiinae and the members of clade 47 are unique only in possessing a broad marginal flange to the dorsal tegular arm (56). However, as noted earlier, the states of this character are not clear cut and may be subject to reinterpretation. A better character is the possession of a pleural pouch (178), although this must be interpreted as having been lost in *Magusa*.

Thus, although clade 47 is a reasonable candidate for the sister-group of the Plusiinae, the evidence is far from unequivocal. Further analysis is necessary, including a detailed study of the relationships of the taxa comprising clade 47, before the sister-group of the Plusiinae can be named with any degree of certainty.

Clade 47 [*20(2)*, 22(0), *23(1)*, *26(1)*, *34(1)*, *37(1)*, *81(0)*, *82(1)*, 83(3), 107(1), 118(0), 156(1), 210(1)]. There are seven good synapomorphies to unite the Stictopterinae, Euteliinae and *Magusa* into a monophyletic group: scale bases on the wings arranged into regular transverse lines (20); bulbous eyes and a prominent frons (23, 26); the setae on the proboscis continuing almost to the apex (34); a smooth ventral edge to the basal two segments of the labial palps (37); and the form of the hair pencils (81) and St8 (82). In addition, the apex of the pleurite is recurved over the tegumen arm to articulate in a pocket on the inner edge (118; also seen in *Calophasia*); the aedeagus is very small compared to the rest of the genitalia (156; reversed in *Paectes*); and there are regular ridges on the corpus bursae (210; present also in *Calophasia* and *Cucullia*).

However, the monophyly of clade 47 should not be accepted uncritically, given the paucity of included genera examined. Although *Magusa* and *Stictoptera* look very alike superficially, experience of similar situations in the Plusiinae (e.g. *Anagrapha* and *Macdunnoughia confusa*) suggests that this may be a poor guide to close cladistic relatedness. The genitalia of *Stictoptera* and *Magusa* in both sexes are very different. Also, *Magusa* is a trifine, with rudiments of a trifine hair pencil (75), whereas the stictopterines and euteliines are unequivocally quadrifine with no trace of trifine hair pencil components. Although these characters may be prone to frequent reversal and convergence, they do suggest that the support for clade 47 may not be as convincing as it may first appear. Also, the sternal hair pencils of *Magusa* are markedly more complex than any seen in the Stictopterinae and Euteliinae, and studies to confirm the homologies proposed in the current investigation are required. Thus, while there can be little doubt that the Stictopterinae and Euteliinae are sister-taxa (see below), the conclusion that *Magusa* is their sister-group must still be considered open.

Clade 48 [13(0), *14(3), 15(0),* 17(1), 18(0), *25(1),* 43(1), 52(2), *57(1), 62(1), 66(1),* 68(1), *70(1),* 72(1), *73(3),* 114(1), 123(1), *153(1), 161(1), 179(1),* 180(1), 190(1), 195(1), 202(1), 211(1)]. Next to the Abrostolini, clade 48, the Euteliinae + Stictopterinae, is the best corroborated clade found in this study. There are no fewer than 11 unique and unreversed synapomorphies to support it, together with a further nine in which the apomorphic state has been subsequently lost in one of the included genera and another four where a convergent development has been recorded in only a single genus outside the clade.

The euteliines and stictopterines share the following good synapomorphies: a reduced female frenulum (14), a full quadrifine hindwing venation (15; probably synapomorphic only in the context of the taxa included in this study, but, given *Magusa* is trifine, maybe a reversal); a frons scaled only at the edge (25); a patagium with a drawn-out attachment point (57); weak SV and V hind basitarsal spines (62); hindlegs shorter than the midlegs (66); dorsal furcal arms that are curved posteriorly (70); the form of the internal flange on T2 (73); ventrally or subventrally positioned valves (153); a small, oval plate in the ductus ejaculatoris (161); and anal papillae in which the inner surfaces are turned to face at least partially posteriorly (179). In addition, the Stictopterinae show partially-developed 'wings' on the proboscis styloconic sensilla (33) (Fig. 113). If this condition is interpreted as intermediate between the plesiomorphic state 1 (Fig. 112) and the apomorphic state 2 (Figs 114–116), then it further corroborates the monophyly of both clade 48 and the Euteliinae.

They also share the following putative synapomorphies but these are either lost in one of the constituent taxa (indicated by '– genus' in parentheses) or occur in another genus outside clade 48 ('+ genus' in parentheses). The character states involved are: underside of the forewing cell without setose scales (13, + *Chalcopasta*); forewing vein $R_2+R_3+R_4$ markedly converging on R_1 then curving away distally (17; – *Paectes*); vom Rath's organ conspicuously papillate (43; – *Anuga*); ventral arm of the tegula spatulate (52; – *Stictoptera*); hindleg inner apical spurs approximately three-quarters length of basitarsus (68; – *Lophoptera*); abdomen distinctly tapered posteriorly (72; – *Lophoptera*); dorsal and ventral flanges of vinculum arms fused across to give a flattened, cone-shaped structure (114; + *Rachiplusia*); vinculum and tegumen broadly joined, pleurite completely fused to tegumen (123; + *Diloba*); inner surface of the anal papillae densely setose (180; + *Calophasia*); anterior apophyses absent (190; – *Stictoptera*); female T8 ventrally produced anteriorly to lie alongside antrum dorsally and exceeding it (195; – *Stictoptera*); female T8 represented by a thin band dorsally (202; – *Stictoptera*); and the corpus bursae with an invaginated signum (211; – *Anuga*).

Examination of the preceding 13 characters reveals that there is no strong pattern to the homoplasies that would imply that either subfamily is paraphyletic relative to the other. It could be argued that *Lophoptera* is more closely related to the euteliines than it is to *Stictoptera*, because it shares four putative synapomorphic features missing in *Stictoptera* (52, 190, 195, 202). However, there are two character states (68, 72) that imply the opposite relationship and, given that there are other characters to corroborate the monophyly of the two subfamilies, the six states just mentioned must be interpreted as homoplasies. Certainly, no firm conclusions should be drawn about the internal structure of clade 48 when only 4 of the 40 or so generic-level taxa have been examined, but equally, I think it is unlikely that the monophyly of the Stictopterinae and of the Euteliinae will be refuted.

Although Hampson (1912) recognized the reduced female frenulum in the Stictopterinae and Euteliinae, he misinterpreted its structure in the latter group, referring to it as being 'single'. He considered the two subfamilies to be parallel developments from the 'Ophiderinae'. Seitz (1937) also observed that the euteliines and stictopterines had a number of features in common, including the large, bulbous eyes (23), from which he concluded that they were closely related.

The recognition of a close relationship suffered a setback with Richards' (1932) study of the tympanal organs of noctuids. He observed a secondary tympanal hood (pleural pouch) in the stictopterines and the plusiines and derived the latter from the former. The euteliines were thought to have much in common with the acontiines and although a membranous secondary tympanal hood was observed in *Eutelia*, the connection with the Stictopterinae (and Plusiinae) was not made. Forbes (1954) referred only to the stictopterine-plusiine relationship, suggesting that these two subfamilies might perhaps be combined, and the euteliine-stictopterine connection was lost.

Recently, in a study of several Bornean noctuid subfamilies, Holloway (1985) resurrected the hypothesis of a euteliine-stictopterine connection when he noted the presence of a small, oval sclerotization in the ductus ejaculatoris (character 161) of the members of these two subfamilies. He also noted several other interesting similarities (e.g. the morphology of the anal papillae) and these formed the basis of the characters employed in this study.

Clade 49: the Stictopterinae [*8(1), 14(5),* 61(1), *62(2),* 121(1), *151(1), 181(1)*]. Five unique and unreversed synapomorphies were found for the two stictopterine genera included in the data set. These are: a hyaline

hind wing base (8); a female frenulum reduced to a single seta (14); suppressed SV and V spines on the basal half of the hindbasitarsus (62); a deeply cleft valve (151); and apically 'frayed' anal papillae (181). Of these, not all stictopterines show the apomorphic states of characters 8 (e.g. *Odontodes*) and 151 (e.g. the *Lophoptera khasiana* Warren species-group) (Holloway, 1985). Character 62 requires confirmation from the other genera but Holloway (1985) found all Bornean stictopterines to have the apomorphic states of characters 14 and 181. To these he added three more putative synapomorphies: the form of the tympanal hood, the general wing facies and a distinctive Y-shaped pupal cremaster (Gardner, 1948*b*). The monophyly of the subfamily thus seems reasonably well corroborated.

Holloway also provided brief reviews of the morphology (both of adults and immatures), biology and zoogeography of the subfamily. In particular, he concluded that the two major lineages of stictopterines have different larval foodplant preferences. The *Stictoptera* genus-group appears to be restricted to members of the Clusiaceae (Guttiferae), while the *Lophoptera* genus-group is primarily recorded from the Dipterocarpaceae. According to Thorne (1976) and Heywood (1978), these two families are closely related, both being members of the Theales, but more recent classifications of the angiosperms (Dahlgren, 1983; Thorne, 1983) disagree, placing the dipterocarps in the Malvales. Members of the *Stictoptera* genus-group may be of potential economic importance as defoliators of crop trees such as *Garcinia* (mangosteen) (Holloway, 1985).

Clade 50: the Euteliinae [*33(2), 35(2), 36(1), 46(1), 47(0),* 58(1), *68(2),* 71(1), *74(1),* 107(0), *115(1), 122(1), 129(1),* 148(0), *152(1),* 157(1)]. The Euteliinae are even better defined and more autapomorphic than their sister-taxon, with no fewer than ten unique and unreversed synapomorphies to corroborate their monophyly. Only *Paectes* and *Anuga* were found to possess the following features: winged styloconic sensilla on the proboscis (33) (but see clade 48 above), which is nodular only at the extreme apex (35) and has regular, dense, basal rows of microspines (36); asymmetrical, bipectinate male antennae (46), with the pectinations bearing only a single, small, apical seta (47); hindleg inner apical spurs that equal or exceed the hind basitarsus in length (68); two internal flanges on St2 (74); vinculum arms that are distally parallel or convergent (115); socii (122); a crescent- or boomerang-shaped, weakly sclerotized juxta (129); and a somewhat trapezoid valve (152).

Of these, however, the antennae are ciliate or filiform in *Anigraea* Walker and *Targalla* Walker respectively; the valves of other genera are more varied in shape; and socii are frequently absent (Holloway, 1985). Many of the other characters listed above require confirmation but all genera appear to possess the flanges on St2, which may be associated with the characteristic resting position of the adults (Holloway, 1985; Kitching, 1984).

Reviews of the morphology of the adults and immatures, biology and zoogeography of the Euteliinae have been presented by Holloway (1985). The lack of a pupal cremaster and a bias towards the Anacardiaceae as larval foodplants (but see also Peigler, 1986) may also represent potential apomorphies for the subfamily. Several genera have been recorded as agricultural pests, especially of mango (*Mangifera*).

Holloway (1985) did not propose a cladistic hypothesis for the euteliine genera. Mell (1943) recognized four genus-groups based on *Penicillaria* Guenée (as *Bombotelia* Hampson), *Eutelia* Hübner (as *Phlogophora* Treitschke), *Anuga*/*Mimanuga* Warren and *Paectes*, but only examined a very small number of species. Thus, the internal relationships of the Euteliinae remain to be elucidated.

Clade 55 [20(0), *21(1), 31(0), 32(2), 34(2),* 46(2), *55(1),* 71(1), 96(1), *208(1)*]. The position of the enigmatic genus *Diloba*, and its single species, *D. caeruleocephala*, has changed with almost monotonous regularity. I gave a brief historical review (Kitching, 1984), charting its course from the Bombyces, via the Noctuidae: Bombyciformes, Notodontidae: Dilobinae, Noctuidae: Plusiinae, Thyatiridae, Noctuidae: Acronictinae, Noctuidae: Pantheinae, Lymantriidae and Dilobidae, to the Noctuidae: Cuculliinae. *Diloba* has certainly been around!

Possible inclusion in the Cuculliinae was first mooted by Tams (quoted in Varley, 1962), who suggested a relationship with the American genus *Psaphida* Walker. Minet (1982), in a critique of Kiriakoff's (1970) work on the tympanal organ of *Diloba*, independently hypothesised a place for the genus in the Cuculliinae, associating it with *Episema* Ochsenheimer. In this study, I decided to follow up Tams' suggestion to test the relationships of *Diloba*. The members of the cuculliine tribe Psaphidini are mostly Nearctic and poorly represented in the BMNH collection. However, specimens of the Holarctic genus *Brachionycha* are more numerous, and this taxon was chosen to represent the Psaphidini, although there have been reservations concerning its placement in this tribe (Forbes, 1954).

I found six putative synapomorphies that were unique to *Brachionycha* and *Diloba*. These would appear to confirm the place of the latter in both the Noctuidae and the Cuculliinae. However, a more extensive

investigation is required to confirm the relationship of these two genera with the Psaphidini and/or *Episema*. The synapomorphies are: the presence of a vestigial remnant of forewing vein *CuP* (21); a reduced, non-functional proboscis with no distal styloconic sensilla and setae continuing to the apex (32, 31, 34); the ventral arm of the tegula produced on a lateral extension of the main body (55); and an apparently small corpus bursae, but with extremely elastic walls (208).

Some of thse conditions are somewhat unconvincing as synapomorphies (especially the reduction characters) but the unusual tegulae have not so far been found elsewhere. There are numerous differences between the two genera but it was not expected that *Brachionycha* would prove to be the sister-group of *Diloba*. However, I hope that I have shown that future studies of the relationships of *Diloba* should concentrate on the Psaphidini and not on the supposed notodontid connection.

Consensus classification

From the preceding evaluation of the preferred 648-step cladogram, it is clear that there are both clades and characters of highly dubious value. For example, the apomorphic state of character 59 has been gained and lost six times, while the monophyly of clade 38 is supported by only a single state change in a character (105) that has a very low consistency index (0·111). For this reason, I performed one final analysis of the data set and will base my classification of the Plusiinae on this, rather than on the preferred 648-step cladogram.

Analytical procedure

The data set was modified for re-analysis as follows. I considered the monophyly of the Plusiinae to have been reasonably well-demonstrated and thus decided to remove the 11 outgroup taxa from the matrix. This also allowed me to exclude 55 characters that exhibited state changes only among the outgroups. These were: 8, 13, 17, 21, 23, 25, 26, 27, 30, 34, 36, 37, 38, 40, 43, 44, 45, 48, 53, 54, 55, 56, 57, 62, 66, 67, 68, 69, 70, 71, 72, 74, 75, 81, 82, 96, 115, 122, 123, 129, 135, 151, 152, 153, 156, 161, 179, 180, 181, 190, 195, 202, 208, 210 and 211. A further five characters (20, 22, 46, 47, 114) were discarded because, after removal of the outgroups, they became autapomorphic for a terminal taxon within the Plusiinae. Finally, all characters that showed consistency indices of $\leq 0{\cdot}250$ were deleted from the data set (5, 6, 12, 16, 18, 19, 42, 58, 59, 105, 107, 110, 144, 162, 191, 196, 201, 205, 209), with the following additions and exceptions. Characters 65 ($c = 0{\cdot}750$) and 83 ($c = 0{\cdot}313$) were also removed. There were doubts regarding the distinction of the states of the first; while the second (male sternal hair pencil development) showed substantial homoplasy, and its relatively large consistency index is due, in part, to the large number of states (5) scored. Ten characters were also left in the matrix despite having consistency indices of $\leq 0{\cdot}250$: 3, 41, 97, 108, 131, 141, 148, 149, 189, and 214. These were generally characters that exhibited homoplasy only within the Plusiinae. Their apomorphic conditions also helped define high level clades in the preferred 648-step cladogram and might, therefore, be expected to exert a significant influence in a re-analysis. For example, 141 appears to be potentially important in the Autoplusiina, while 189 concerns the possible relationship between *Syngrapha* (s.l.), *Anagrapha* and clade 30.

As before, *Shensiplusia* was also omitted from the analysis.

Finally, the removal of the outgroups allowed character 14 to be analysed as an ordered character; all other unordered characters were treated as before.

The analysis was performed using the PAUP options HOLD = 3, SWAP = GLOBAL, MULPARS, NORELEASE; all other options being set to their default values. It was hoped that the deletion of about one-fifth of the taxa and over a third of the characters would speed up the computations. However, the opposite result was obtained; the analysis slowed considerably and took an almost excessive amount of computing time. I would therefore suggest that if anyone intends to delete such a large amount of data 'in program', as was done here, then they circumvent the tree-building routine, which took most of the time, by entering a USER-TREE that is expected to approximate the end result and perform branch-swapping on that topology. An even better approach would probably be to recast the data physically to remove the required taxa and characters and analyse this smaller data matrix. Either of these techniques should decrease the run times of large reduced data sets significantly.

Results

As might have been expected, the MAXTREE default maximum of 50 cladograms was obtained. They were 301 steps in length and had consistency indices of 0·584. Two observations can be made from these figures. First, exclusion of the outgroups and characters of low consistency eliminated over half the steps of the earlier cladograms (i.e. 346 of the original 647). However, the consistency index did not rise by as much

as perhaps might have been expected, 0·475 to 0·584. This is primarily because the rise in consistency due to the loss of the low consistency characters was counterbalanced to some degree by a lowering in consistency due to the loss of many high consistency characters concerned with the outgroup interrelationships.

Examination of the 50 cladograms revealed a series of alternative subtopologies similar, but not identical, to those obtained for the 648-step cladograms. (The clade numbers used subsequently are those employed on the preferred cladogram and imply the same constituent taxa, though not necessarily the same topology.)

First, the positions of *Agrapha* and *Plusiopalpa* varied. Three alternative topologies were recorded. On the first, *Plusiopalpa* is placed as the sister-group of *Argyrogramma* + *Stigmoplusia*, with *Agrapha* as the sister-group of *Ctenoplusia* + *Acanthoplusia*. The other two topologies are the same as those found for clade 14 on the 648-step cladograms (see above).

Dactyloplusia has moved to become the sister-group of *Thysanoplusia*, rather than, as before, forming the sister-group of *Chrysodeixis* + *Pseudoplusia*. This new clade is placed either as the sister-group of *Trichoplusia* or as the sister-group of *Trichoplusia* + clade 12. Otherwise, the Argyrogrammatini display the same topology as the preferred 648-state cladogram.

In the Euchalciina, there is ambiguity as to the position of *Panchrysia* + *Chrysanympha*. One subtopology places this clade as the sister-group of *Euchalcia* + *Adeva*, while the other treats it as the sister-group of clade 24, as on the preferred cladogram. Otherwise the Euchalciina is unchanged.

The exclusion of the characters of low consistency, as might have been expected, had a significant effect upon the topology of the Autoplusiina and Plusiina. Clade 30 is recovered by and large intact, although *Loboplusia* is placed as the sister-group of clade 32 + 35, with *Erythroplusia* as the sister-group to this clade. However, *Loboplusia* and *Erythroplusia* can exchange positions.

At the base of the Autoplusiina, and within the Plusiina, there is what can only be described as near chaos, with at least 13 alternative subtopologies being found. *Syngrapha* (s.l.) is recovered intact as before. A new clade is also consistently obtained, comprising two pairs of taxa in a sister-group relationship; *Lophoplusia* + *Plusia* and *Autographa bractea* + *Cornutiplusia*. However, the relationships of these, *Autographa gamma*, clade 30, *Anagrapha*, *Rachiplusia* and *Diachrysia* appear to be able to take on any form. For example, at one extreme, *Anagrapha* forms the sister-group of *Rachiplusia*, which together form the sister-group of the rest of the Autoplusiina, while *Diachrysia* forms the sister-group of clade 39. At the other extreme, clade 37 is recovered intact but *Rachiplusia* is interpreted as the sister-group of clade 30 + 37. Numerous other alternative subtopologies were found, most of which comprise variations on the placements of *Anagrapha*, *Rachiplusia* and *Diachrysia*. Such a result was not unexpected in view of the evaluation of these taxa performed above and the characters deleted in the present analysis.

Along the main stem of the cladograms, no change in the topology was expected nor found. The cladistic relationships among the tribes and subtribes is identical to that of the preferred 648-step cladogram, namely: (Omorphinini (Abrostolini (Euchalciina (Autoplusiina + Plusiina)))).

To extract the maximally predictive classification of the Plusiinae from these alternatives, a manual strict (Nelson) consensus cladogram analysis (Nelson, 1979) was performed. The ambiguity in clade 14 is reduced to a terminal tetrachotomy between *Plusiopalpa*, *Agrapha*, *Argyrogramma* + *Stigmoplusia* and *Ctenoplusia* + *Acanthoplusia*. Similarly, trichotomous relationships are assumed between clade 12, *Trichoplusia* and *Thysanoplusia* + *Dactyloplusia*; and between clades 23, 25 and 26 in the Euchalciina. *Rachiplusia* is removed from the Autoplusiina and placed with *Anagrapha* and *Diachrysia* in a pentachotomous relationship with clades 30 and 37. This best reflects the uncertainty of relationship of the three single genera concerned. Within clade 30, *Loboplusia* forms a trichotomy with *Erythroplusia* and clade 32 + 35; while in clade 37, *Autographa gamma*, *Syngrapha* (s.l.) and *Lophoplusia*/*Plusia*/*Autographa bractea*/*Cornutiplusia* are also trichotomously related.

Finally, in recognition of the fact that, on the preferred 648-step cladogram, neither clade 12 nor clade 14 was supported by good synapomorphies, and that, for example, blade-like valve setae (133) may eventually prove to be a good synapomorphy for clades 13 and 16, the branches subtending clades 12 and 14 were collapsed, leaving a terminal heptachotomy within the Argyrogrammatini. This consensus cladogram (with the addition of *Pseudochalcia*, *Desertoplusia* and *Shensiplusia*; see below) is shown in Figs 29, 30, and will form the basis of the formal higher classification of the Plusiinae presented in this study.

The positions of *Shensiplusia*, *Desertoplusia* and *Pseudochalcia*

Shensiplusia. *Shensiplusia* was described by Chou & Lu (1974) to accommodate the species *S. nigribursa*, known only from the holotype female. It was said to resemble *Argyrogramma* (in the broadest sense) and, specifically, to be very similar in external appearance to *Acanthoplusia* (as *Argyrogramma*) *agnata*. *S. nigribursa* differed in being larger and in having more metallic iridescent scaling on the forewings. This

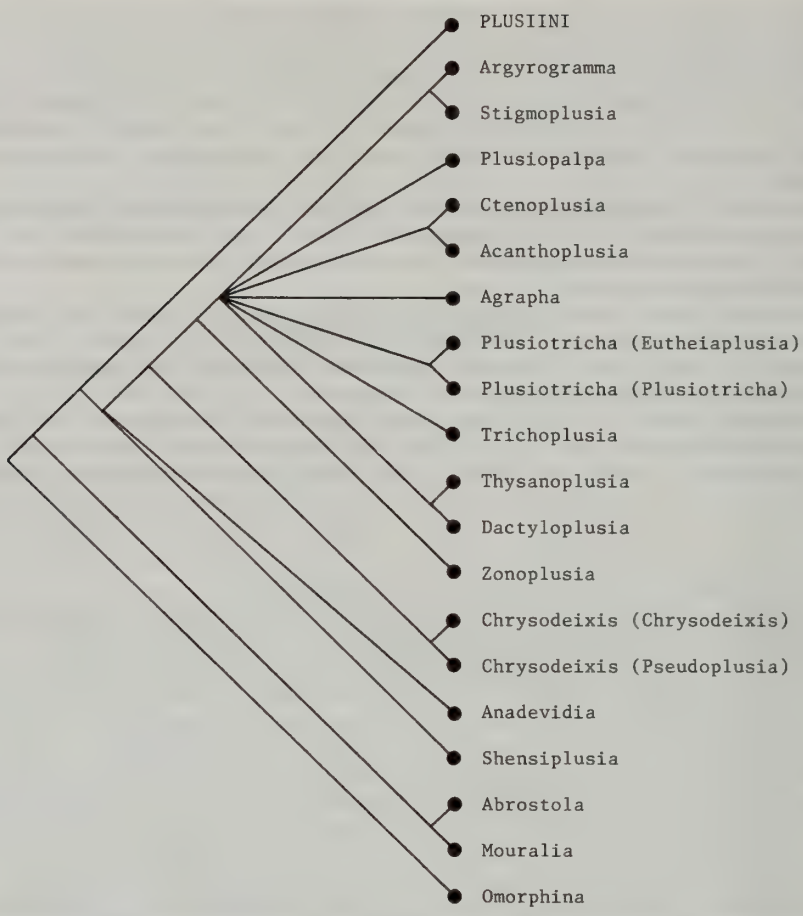


Fig. 29 The consensus classification of the tribes Omorphinini, Abrostolini and Argyrogrammatini. The genus *Shensiplusia* is *incertae sedis* in the Argyrogrammatini.

description, together with Chou & Lu's record for discovering 'new' species in China, suggests that *S. nigribursa* may eventually prove synonymous with *A. agnata* or a related species. However, the female genitalia of *A. agnata* figured by Ichinosé (1962*b*: pl. 9, fig. 6) do not correspond exactly to those of *S. nigribursa* (Chou & Lu, 1974: fig. 16). In particular, *A. agnata* does not appear to have the corpus bursae covered internally with the numerous sclerotized spinules that give *S. nigribursa* its name. Chou & Lu (1974) also stated that the corpus bursae of *S. nigribursa* was somewhat similar to that of *Chrysodeixis* (as *Neoplusia*) *acuta*.

Although Chou & Lu provided little information useful in placing *Shensiplusia* within the Plusiinae, it seems likely that the genus is an argyrogrammatine. However, further resolution of its position is impossible at present (in particular, in the absence of the male) and in recognition of this, I have placed *Shensiplusia* at the base of the Argyrogrammatini, in a trichotomy with *Anadevidia* and clade 6 (Fig. 29).

Needless to say, nothing is known of the biology of *Shensiplusia*, except that it was taken at Wukung in Shensi Province, China.

Desertoplusia. I learned of the descriptions of *Desertoplusia* and *Pseudochalcia* (Kljutshko, 1984) too late to include their type species, *D. bella* (Christoph) and *P. inconspicua* (Graeser), in the full analysis. I thus have to be content with placing them as best I can onto the cladogram (Fig. 30) constructed from the other genera. To this end, they will also provide useful tests of the robustness of the arrangement and its supporting characters.

Desertoplusia contains two species, *D. bella* (Fig. 70) and *D. paghmana* (Wiltshire). In superficial appearance, they resemble miniature autographas and were placed in that genus by Wiltshire (1971) and as its sister-group by Kljutshko (1985*b*). However, an examination of the male genitalia of both species, as

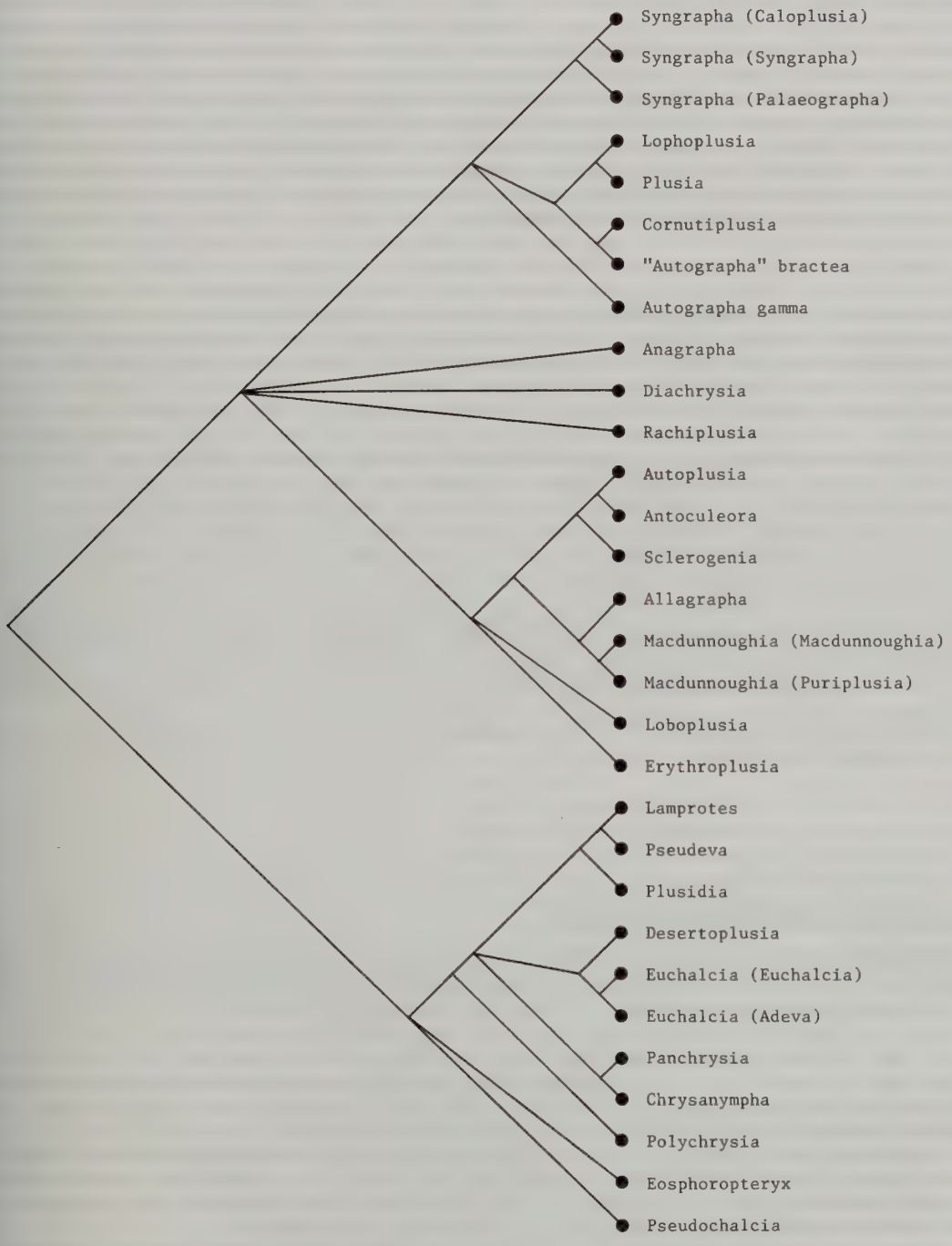


Fig. 30 The consensus classification of the tribe Plusiini, comprising the subtribes Euchalciina, Autoplusiina and Plusiina. The genus *Pseudochalcia* is *incertae sedis* in the Euchalciina, while the genera *Rachiplusia, Diachrysia* and *Anagrapha* are *incertae sedis* in the Autoplusiina + Plusiina. *Loboplusia* and *Erythroplusia* are *incertae sedis* in the Autoplusiina.

figured by Wiltshire (1971), reveals that they have simple oval valves (147), reduced clavi (144:1) and subapical cornuti that arise from circular, concave plates (164). These character states indicate that *Desertoplusia* belongs respectively to clades 21, 24 and 25. However, *Desertoplusia* retains the plesiomorphic plusiine forewing colour pattern and thus in Fig. 30, it is placed as the sister-group of *Euchalcia* + *Adeva*. However, it should be noted that future studies may position the genus internal to clade 25.

D. bella is recorded in the BMNH collection only from Ashkhabad in Turkmeniya S.S.R. *D. paghmana* comprises two subspecies. *D. p. paghmana* is confined to the Paghman Mountains, north-west of Kabul in Afghanistan, while *D. p. paupera* is found only near Quetta, Pakistan (Wiltshire, 1971). Nothing is known about the biology of either species but they appear to be part of the same steppe-montane fauna as *Euchalcia* and *Pseudochalcia*. Being a euchalciine, the larval foodplant is predicted to be a member of the Ranunculaceae or, much less likely, the Boraginaceae.

Pseudochalcia. I mentioned above in the clade analysis that Kljutshko (1984) had erected *Pseudochalcia* to accommodate *P. inconspicua* (Fig. 69), thereby formalizing Dufay's (1968) conclusion that the species did not belong in *Euchalcia*. Kljutshko (1985*b*) interpreted *Pseudochalcia* to be the sister-group of *Euchalcia*, based on the shape of the juxta apex. In both genera, this forms a somewhat recurved, blunt lobe. In this study, however, a similar condition was found in *Diachrysia chryson, Autographa gamma, Erythroplusia rutulifrons, Antoculeora ornatissima, Adeva albavitta* and *Chrysanympha formosa*. Examination of the male and female genitalia figured by Kostrowicki (1961) yields little further data to help place *Pseudochalcia*. The valve is roughly quadrate in shape and thus resembles certain *Euchalcia* species. However, the subapical cornutus is absent, the vesica ornamentation consisting primarily of a transverse row of straight cornuti about halfway(?) along the vesica. The sacculus is armed apically with two short, divergent, sharp points (saccular sheets?) and appears to have a basal, broad triangular point. These features suggest a possible relationship with certain autoplusiine taxa. However, the apex of the corpus bursae is membranous and lacks sclerotized ridges. Thus, like Dufay (1968), I do not know what the detailed relationships of *Pseudochalcia* are. It is certainly a member of the Plusiini and possibly the Euchalciina, although inclusion in the Autoplusiina cannot be entirely ruled out. In recognition of this uncertainty, I have placed *Pseudochalcia* in a trichotomous relationship in the Euchalciina with *Eosphoropteryx* and clade 21 (Fig. 30).

Nothing is known of the biology of *P. inconspicua*. It is restricted to the mountains of Central Asia (Kostrowicki, 1961; Kljutshko, 1984).

The higher classification of the Plusiinae

The formal classification of the plusiine generic and higher level taxa given in Appendix 5 was constructed using the conventions for annotated Linnaean hierarchies defined and described by Wiley (1979; 1981). The hierarchy is fully sequenced (Nelson, 1974), that is, 'taxa forming an asymmetrical part of a phylogenetic tree may be placed at the same categorical rank and sequenced in phylogenetic order of origin' (Wiley, 1981: 209). This has the effect of reducing the number of named subordinate taxa, the proliferation of which has long been a target for anti-cladists (e.g. Colless, 1977). I have reduced this number further by adopting informal genus-groups and, twice, genus-complexes. This approach was adopted because of the intrinsic uncertainty regarding several areas of the underlying cladogram.

Taxa forming parts of polytomies 'are given equivalent ranks and placed *sedis mutabilis* at the level of the hierarchy at which their relationships to other taxa are known' (Wiley, 1981: 211). This convention differentiates those parts of the sequences that are dichotomous from those that are polytomous. It indicates that the taxa labelled *sedis mutabilis* are of interchangeable position.

Finally, five genera were identified as being *incertae sedis*, of uncertain position. They are 'placed in the hierarchy . . . at the level their relationships are best understood' (Wiley, 1981: 212). For example, *Shensiplusia* is considered to be an argyrogrammatine, but its sister-group could be the whole tribe or any clade within the tribe. It is thus placed *incertae sedis* at the level of the Argyrogrammatini.

The application of these conventions allows the construction of a Linnaean hierarchy from which the structure of the underlying cladogram is immediately apparent. Further conventions were formulated by Wiley (1979; 1981) but were not necessary in the present context.

The Plusiinae are divided into four tribes: the monotypic Omorphinini Chou & Lu, the Abrostolini Eichlin & Cunningham, the Argyrogrammatini Eichlin & Cunningham and the Plusiini Boisduval. The Abrostolini comprises two genera, *Abrostola* and *Mouralia*.

Within the Argyrogrammatini, as noted above, *Shensiplusia* is placed *incertae sedis*. The first level of sequencing comprises three genera (*Anadevidia, Chrysodeixis* and *Zonoplusia*) and the terminal *Argyrogramma*-complex of genera and genus-groups. *Chrysodeixis* contains two subgenera, *Chrysodeixis* (s.str.) and *Pseudoplusia* **stat. n.** The *Argyrogramma*-complex consists of seven lineages, all placed *sedis mutabilis*. These consist of five genera (*Trichoplusia, Plusiotricha, Ctenoplusia, Agrapha* and *Plusiopalpa*) and two genus-groups. Genus-groups were erected generally where the evidence in favour of synonymy was considered inadequate. Thus *Thysanoplusia* **stat. rev.** and *Dactyloplusia* are placed together in the *Thysanoplusia* genus-group, and *Argyrogramma* and *Stigmoplusia* in the *Argyrogramma* genus-group. In contrast, *Eutheiaplusia* **stat. n.** and *Acanthoplusia* **stat. rev.** are reduced to subgeneric rank within *Plusiotricha* and *Ctenoplusia* respectively. This approach, rather than full synonymy, was adopted because I consider that both *Eutheiaplusia* and *Acanthoplusia* represent distinct monophyletic units within their respective genera (see Clade analysis). As concluded above (Clade analysis), and contrary to the (unstated) opinions of Franclemont & Todd (1983), I have found no convincing evidence for accepting a synonymy of *Ctenoplusia* with *Agrapha*. I thus reinstate *Ctenoplusia* **stat. rev.** as a genus separate from *Agrapha*.

The Plusiini is divided into three subtribes: the Euchalciina Chou & Lu, the Autoplusiina **subtrib. n.** and the Plusiina Boisduval.

Within the Euchalciina, *Pseudochalcia* is placed basally *incertae sedis*. The first level of sequencing comprises *Eosphoropteryx, Polychrysia* and the *Panchrysia, Euchalcia* and *Lamprotes* genus-groups. The last three of these are placed *sedis mutabilis*. They contain, respectively, *Panchrysia* and *Chrysanympha, Desertoplusia* and *Euchalcia*, and (sequenced) *Plusidia, Lamprotes* and *Pseudeva*. Following the suggestions of Kostrowicki (1961), Dufay, (1968) and Franclemont & Todd (1983), *Adeva* is placed within *Euchalcia*, but as the subgenus *Euchalcia (Adeva)* **stat. n.**, until such time as the internal structure of *Euchalcia* (s.str.) is resolved.

Although the taxon Autoplusiina + Plusiina is not formally named, three genera are placed *incertae sedis* at this level in the hierarchy. *Rachiplusia* will probably be shown eventually to belong to the Autoplusiina but I can only speculate that this may also be the correct tribe for *Anagrapha* and *Diachrysia*.

Within the Autoplusiina, *Erythroplusia* and *Loboplusia* are placed basally *incertae sedis*. The remaining two genus-groups form a fully dichotomous and sequenced clade. The *Autoplusia* genus-group comprises *Sclerogenia, Antoculeora* and *Autoplusia*; the *Macdunnoughia* genus-group consists of *Allagrapha* and *Macdunnoughia*. The latter genus includes *Puriplusia* as a subgenus.

Three groups are recognized within the Plusiina, in trichotomous relationship. That represented by *Autographa gamma* is probably paraphyletic and requires further work. *Syngrapha* (s.l.) is recognized as a monophyletic group comprising three sequenced subgenera (at least): *Palaeographa, Syngrapha* (s.str.) and *Caloplusia* **stat. rev.** The final taxon in this group is the *Plusia*-complex, comprising two genus-groups based upon *Plusia* and *Cornutiplusia* **stat. rev.** The former also includes *Lophoplusia* **stat. n.**, the latter, the group of *Autographa* represented by *A. bractea*. Given that there is at least one further lineage within that genus (those species possessing seta SV2 on segment A1 of the larva), *Autographa* is at least triphyletic and ought eventually to be subdivided. Until a thorough investigation is undertaken, however, formal naming of the various lineages should be avoided.

Comparison with previous classifications and phylogenies

After Eichlin & Cunningham (1978) proposed their phylogeny of the Nearctic Plusiinae, they noted that although it and those of Kostrowicki (1961) and Ichinosé (1962*b*) had been 'derived independently . . . studying different faunal areas . . . the basic evolutionary lines are essentially the same'. Subsequently, two further dendrogrammatic representations of the higher classification of the Plusiinae were published (Chou & Lu, 1979*c*; Kljutshko, 1985*a*; *b*). A comparison of these five hierarchies with that proposed in the present study shows that Eichlin & Cunningham's observation still, by and large, holds true. However, there are discrepancies between each and my own conclusions that deserve brief discussion.

Kostrowicki (1961) (Fig. 1 v Figs 29, 30). Kostrowicki's study was, by a narrow margin, the first new attempt to analyse the higher classification of the Plusiinae since Hampson (1913). It was based upon the Palaearctic fauna and thus included very few representatives of the primarily tropical Argyrogrammatini.

If it is assumed that Kostrowicki would have converted his 'scheme of relationships' directly into a classification (which is unlikely but a necessary assumption if a meaningful comparison is to be made), then the following points of concordance and disagreement with my classification can be noted.

Abrostola and *Mouralia* were considered to be the most primitive group of plusiines (stated implicitly). *Omorphina* was erroneously transferred, without explanation, to the Acontiinae (as Erastriinae). Within the Plusiinae examined, Kostrowicki's first split was into two groups roughly corresponding to the Autoplusiina + Plusiina and the Euchalciina + Argyrogrammatini. Misidentifications allowed him to misplace *Macdunnoughia* in the Argyrogrammatini, while the other two autoplusiine genera considered, *Rachiplusia* and *Autoplusia*, were treated together as the closest relatives of *Cornutiplusia*. *Chrysanympha* was mistakenly associated with *Plusia*, from which it was supposed to have been derived. The Plusiina was thus paraphyletic. The topology of the genera of this subtribe was similar to that in Fig. 30 but both *Plusia* and *Cornutiplusia* branched off before *Autographa*, and *Anagrapha* was associated with *Syngrapha* (s.l.).

Within the Euchalciina (which included *Diachrysia*), a similar topology to that in Fig. 30 was found. However, the branching sequence for the *Lamprotes* genus-group was inverted and *Panchrysia* was placed with *Polychrysia*.

The Argyrogrammatini, with the exception of *Anadevidia*, was monophyletic (allowing for *Macdunnoughia*, see above), but *Chrysodeixis* was associated with *Argyrogramma* rather than with *Pseudoplusia*. *Anadevidia* was treated as the sister-group of the rest of the Argyrogrammatini + Euchalciina.

Overall, most of the tribes and subtribes (with the exception of the Autoplusiina) are represented reasonably accurately on Kostrowicki's phylogenetic scheme. However, their interrelationships and several of the generic assignments are at considerable variance with subsequent classifications.

Ichinosé (1962*b*) (Fig. 2 v Figs 29, 30). Following very shortly after that of Kostrowicki (1961), Ichinosé's (1962*b*) scheme of Japanese plusiine systematics represented a significant improvement due primarily to the inclusion of *Abrostola* in the study. The recognition of this genus as the most 'primitive' plusiine taxon examined resulted in Ichinosé reconstructing the first few branch-points within the subfamily more accurately than Kostrowicki. Nevertheless, the Argyrogrammatini were paraphyletic, with *Chrysodeixis* (sensu *Trichoplusia* (s.str.), *Chrysodeixis* (s.str.) and *Ctenoplusia* (s.l.)) branching off first, followed by a pentachotomy consisting of *Ctenoplusia (Acanthoplusia)* (as *Chrysodeixis*) *agnata, Thysanoplusia* + *Anadevidia, Diachrysia,* the Euchalciina and the Autoplusiina + Plusiina. As for Kostrowicki, this interpretation of Ichinosé's diagram requires its conversion into cladogram form. The original consisted of a series of interconnected circles and thus had numerous extant taxa as putative ancestral forms to other extant taxa. Hence some of the branches are zero-length projections (e.g. the branch subtending *Ctenoplusia (Acanthoplusia) agnata*). The Euchalciina and the Plusiina were less well-resolved topologies of those found in the present study, while the Autoplusiina (represented by *Erythroplusia* and *Macdunnoughia* (s.l.) (including *Sclerogenia* and *Antoculeora*) was paraphyletic.

Thus Ichinosé's scheme shows a considerable degree of concordance with that proposed here. The discrepancies can be largely attributed to his inclusion of only two character complexes in the construction of his systematic arrangement – larval chaetotactic 'plan' and the presence/absence of abdominal dorso-lateral hair tufts in the males. This accounts for why *Chrysodeixis* (sensu Ichinosé) was biphyletic and the Plusiini were not recognized as a monophyletic group (*'C.' agnata* lacks vestigial larval prolegs on segments A3 and A4), and why the Autoplusiina were paraphyletic (both *Macdunnoughia* [sensu Ichinosé's *'Scleroplusia'*] and *Autographa* are heterogeneous regarding the presence/absence of seta SV2 on segment A1). In fact, Ichinosé's interconnected circles are probably more correctly interpreted as depicting the supposed evolution of plusiine larval chaetotaxy than of the Plusiinae themselves.

Eichlin & Cunningham (1978) (Fig. 3 v Figs 29, 30). Eichlin & Cunningham's (1978) phylogeny of the plusiines is by far the best published approximation to my own results. It incorporated both larval and adult characters, with little apparent bias towards either, although the explicit use of some characters was often unstated. The result was remarkably congruent with my own. All the tribal and subtribal groups confirmed in this study were first recognized by Eichlin & Cunningham, with the exception of the Euchalciina and the clade Autoplusiina + Plusiina.

Thus, the Abrostolini were placed as the most primitive tribe, followed by the basic subdivision of the plusias into the Argyrogrammatini and Plusiini. Further analysis of the former was hindered by their virtual absence from the Nearctic fauna, only five species from three genera occurring north of Mexico. The Autoplusiina were the first to branch off the Plusiini lineage. *Rachiplusia* and *Diachrysia* were interpreted as the sister-groups of *Autoplusia* and *Allagrapha* respectively, conclusions that are consistent with, if not entirely supported by, my own results. The branching sequence of *Polychrysia, Adeva* and *Pseudeva* was identical (allowing for missing Palaearctic taxa) but *Chrysanympha* and *Eosphoropteryx* were misplaced as

possible branches from the Plusiina. However, Eichlin & Cunningham were unsure of the position of these genera.

The non-monophyletic nature of *Autographa*, confirmed in the present study (if not in the manner originally intended!), was first explicitly noted by Eichlin & Cunningham, although it must be said that this conclusion was implicit in Ichinosé's (1962*b*) scheme. Eichlin & Cunningham's (1978) arrangement of *Plusia* and *Syngrapha* (s.l.) agrees more or less with my own, as far as the two are comparable, with the exception of their positioning of *Anagrapha* within *Syngrapha*. Their conclusions might have been different had *Macdunnoughia* occurred in North America.

Chou & Lu (1979*c*) (Fig. 4 v Figs 29, 30). The phylogeny of the Plusiinae proposed by Chou & Lu (1979*c*) represented a retrograde step in the systematics of the Plusiinae. It was overtly phenetic in derivation, very poorly resolved and based upon relatively few characters, several of which were of very dubious quality and reliability. However, they did recognize *Omorphina* (Omorphinini) as the most basal plusiine lineage, followed by the Abrostolini (*Abrostola*). If their 'Plusiini' (*Diachrysia, Anadevidia, Thysanoplusia*) is ignored, then the Argyrogrammatini is recovered intact, though it also includes *Erythroplusia* and *Puriplusia*. The Euchalciina is also regarded as monophyletic. However, the internal relationships of these two groups bear only minimal correspondence with my results. *Syngrapha* (s.l.) was interpreted as a lineage independent of the Plusiina + Autoplusiina (less *Puriplusia* and *Erythroplusia*). Thus, despite inadequate methods and reliance upon a few tried-and-tested 'classic' characters, several of the most robust plusiine clades did emerge intact from Chou & Lu's analysis.

Kljutshko (1985*a*, *b*) (Figs 5–7 v Figs 29, 30). I described in detail above why Kljutshko's original cladogram (Fig. 5) of the Palaearctic Plusiinae was erroneous. After correctly applying cladistic methodology, the somewhat more polytomous cladogram (Fig. 6) is comparable with my own findings. Like most workers, Kljutshko recovered the Argyrogrammatini (less *Anadevidia*) as a monophyletic unit. The Plusiini were also treated as monophyletic, allowing for the exclusion of *Erythroplusia*. However, the fragmentation of the Euchalciina into four separate lineages resulted in almost complete incongruence between Kljutshko's groupings and my own. The only concordant taxa are *Syngrapha* + *Caloplusia* and the Autoplusiina (represented by *Macdunnoughia* and *Antoculeora*). Reanalysis of some of his characters (Fig. 7) resulted in the gain of only one more congruent clade, the Argyrogrammatini + Plusiini. Overall, a laudable effort at explicit cladistic character analysis but a poor result.

Discussion

Larval foodplant associations

One of the most popular eco-systematic subjects at present is the investigation of the interactions between herbivorous insects and their foodplants. The plusiines show a marked divergence in the number and relationships of the plants that their larvae eat. Of those that are known (a proviso that underlies this entire section of the discussion), many plusiine genera are extremely polyphagous, often giving the impression that a plant merely has to be green, and preferably herbaceous, to be a potential meal. Such genera include *Chrysodeixis, Trichoplusia, Thysanoplusia, Argyrogramma, Allagrapha, Autoplusia, Anagrapha* and *Autographa*, which include most of the notorious agricultural pests of the subfamily.

At the other extreme, a number of genera are known to be virtually monophagous at the level of plant genus. For example, *Lophoplusia violacea* is known to eat only the labiate *Stenogyne*, while its congener, *L. pterylota*, is recorded only from *Clermontia* in the relatively unrelated Lobeliaceae. Many other examples were noted above and can be summarized thus: *Abrostola* (Urticaceae and related families, one species on Asclepiadaceae); *Mouralia* (Commelinaceae); *Anadevidia* (Cucurbitaceae); *Ctenoplusia albostriata* + putative allies (Asteraceae); Euchalciina (most) (Ranunculaceae); *Euchalcia* (part) (Boraginaceae); *Chrysanympha* (Ericaceae); *Erythroplusia, Macdunnoughia, Sclerogenia, Antoculeora, Autographa bractea* + putative allies (all Asteraceae); *Plusia* (monocotyledons); and *Syngrapha celsa* and *rectangula* species-groups (conifers).

The most striking observation about this wide ranging monophagy and oligiphagy is that there is very little pattern to it from the point of view of either plant or plusiine systematics. The sister-group of an oligophagous plusiine genus is about as likely to be polyphagous as oligopha-

gous, and if the latter then it will probably feed on a markedly different group of plants. Compare, for example, the sister-group pairs of *Plusia/Lophoplusia, Abrostola/Mouralia* and *Autoplusia/Antoculeora*. The only two generalizations that can be made are that most euchalciines feed on Ranunculaceae, and oligophagous autoplusiines seem to show a preference for Asteraceae. Many foodplant records are missing for the tropical argyrogrammatines. When their life histories are elucidated, I expect equally varied, interesting and oligophagous patterns to be found as are presently observed in the remainder of the subfamily.

Biogeography

Very little has been published on the biogeography of the Plusiinae, mainly because all of the previous studies have examined isolated faunas. This makes a world-wide comparison and evaluation virtually impossible, especially from the historical viewpoint.

Kostrowicki (1961) presented in detail the descriptive and distributional biogeography of the plusias, concentrating on the Palaearctic species. He noted that the Argyrogrammatini (his group A) were essentially tropical, occurring in the Holarctic region primarily in the southern areas. He considered his group B (*Autoplusia, Rachiplusia, Cornutiplusia*) to be characteristic of Notogaea. Notogaea is defined by the Chambers Twentieth Century Dictionary as Australia, the islands to the north, New Zealand and Polynesia, while the Concise Oxford English Dictionary also includes the neotropics. Neither of these concepts coincides with the range of group B, which is absent from Oceania but present also in Africa, and, to a lesser extent, in the Holarctic. Kostrowicki's group C (*Syngrapha, Caloplusia, Anagrapha*) was exclusively Holarctic (with the exception of one unnamed species in the Andes – presumably *Rachiplusia virgula*, which thus belongs to group B), as was group D (the balance of the plusias), although most species of the latter group were Palaearctic.

Kostrowicki proceeded to examine these distributions in greater detail and speculated on the centres of origin and dispersal routes of the various taxa. Group A was supposed to have originated in the Old World tropics, while group C was of 'obvious boreal-alpine and superficially circum-boreal origin'. Group D was hypothesised to have had its origins in the eastern Palaearctic, where most of its species are currently found. However, lack of a consideration of the Omorphinini and Abrostolini, coupled with a dispersalist/centre of origin approach resulted in much speculative fiction. This was compounded by Kostrowicki's errors of identification and his non-critical systematic analysis.

A better basis for a zoogeographical analysis was Eichlin & Cunningham's (1978) phylogeny. However, their comments on the subject comprised merely a single paragraph. Coloured by their belief that the Plusiinae were very closely related to the Stictopterinae, they postulated a tropical origin for the plusiines, followed by an invasion of the temperate zones. The Argyrogrammatini were again recognized as a primarily tropical tribe, the Plusiini as primarily temperate, some of which had further adapted to Boreal or Arctic conditions.

The results of the present study represent the first attempt to analyse the higher classification of the Plusiinae on a world-wide basis. It would thus probably be seen as unforgivable if I did not make some statements regarding the historical biogeography of the subfamily. However, they will necessarily be non-commital and somewhat conjectural, given the ambiguity contained in the cladogram upon which they are based.

In the absence of a reasonable hypothesis as to the immediate outgroup to the Plusiinae, I can only speculate where the subfamily might have first arisen. Perhaps the marginally most plausible area is the south-eastern Palaearctic/north-eastern Oriental regions. In this area are currently found the most plesiomorphic plusiine, *Omorphina*; the *Abrostola* species (*A. anophioides*) that may represent the intermediate link with *Mouralia*; several of the more plesiomorphic argyrogrammatine genera (notably *Anadevidia* and *Zonoplusia*); and some of the plesiomorphic members of the three subtribes of the Plusiini: *Diachrysia, Erythroplusia, Polychrysia*.

If this hypothesis is accepted, for the sake of argument, then the 'proto-Abrostolini' may have had a more or less world-wide occurrence, with subsequent vicariance events isolating first

Mouralia, then the Nearctic abrostolas. A cladistic analysis of the Abrostolini is necessary to test this suggestion.

It appears most likely that the Argyrogrammatini evolved primarily in the tropics and the Plusiini in the temperate regions. Superficially, this may suggest a Gondwanan and Laurasian distribution pattern respectively. However, it is extremely unlikely that the cladogenetic event that ultimately gave rise to the two major plusiine lineages was contemporaneous with the primary break-up of Pangea. Such an association would place the time of divergence of the Argyrogrammatini and Plusiini at between 180 (Rosen, 1978) and 150 (Irving, 1977) million years ago, that is, in the Jurassic, before the currently accepted origin of the angiosperms! A more recent origin would seem less incredible but remains unknown.

There are other interesting patterns of distribution within the subfamily. *Chrysodeixis* seems to show a good example of a transantarctic distribution. *C. (Pseudoplusia)* is found in South America and Saint Helena, while the hypothesised plesiomorphic *C. (Chrysodeixis), C. argentifera*, is found in Australia. More apomorphic *Chrysodeixis* species are then found towards the Equator. This genus would be one of the most profitable to study from a biogeographic point of view, as well as containing no fewer than five economically important pest species (*C. includens, C. argentifera, C. eriosoma, C. chalcites* and *C. acuta*).

Within the Plusiini, there are several examples of Nearctic/Palaearctic sister-genus pairs: *Chrysanympha/Panchrysia, Euchalcia (Adeva)/Euchalcia* (s.str.), *Pseudeva/Lamprotes, Allagrapha/Macdunnoughia* and *Autoplusia/Antoculeora*. These have only become apparent following a world-wide analysis of the subfamily and all merit further investigation. The conclusion that *Lophoplusia* is the sister-group of *Plusia* implies that the former, a Hawaiian endemic, originated by dispersal from either the eastern Palaearctic or western Nearctic. A decision between the two must await the resolution of the interrelationships of the species of these, and maybe related, genera. Finally, the most apomorphic syngraphas appear to be those that live furthest north, culminating in those with a circumpolar distribution. A cladistic analysis is necessary to reveal whether this northward pattern is truly as linear as it first appears.

All of the above observations are preliminary and tentative, and are meant more as stimuli to further research than as statements of fact. More concrete conclusions must await detailed cladistic investigations of the individual plusiine genera and a more comprehensive analysis of the higher classification. There is no doubt, however, that the Plusiinae could prove to be most rewarding subjects for biogeographical analysis.

Conclusions

Eichlin & Cunningham (1978) concluded with the hope that their study would be useful as a framework for future work. By examining the world fauna, I have endeavoured to synthesize an overall classification that has illuminated transcontinental relationships not suspected from the previous faunal studies. However, this arrangement is also preliminary, as any first attempt in an uncharted field must be. Although I have referred in this paper to over half the plusiine species, I have examined in detail less than one-eighth of them. Many species still languish in '*Plusia*' s.l. and the elucidation of their relationships should have high priority, if only to empty a dustbin. Similarly, *Trichoplusia* ought to be dismembered into its component monophyletic groups but I suspect that an analysis of the 'higher' argyrogrammatines may have to be performed first or simultaneously, rendering this a massive task. The subtribes of the Plusiini are also poorly defined and grey areas often include potential or actual pest species (e.g. *Anagrapha falcifera*). *Autographa*, in particular, is in dire need of attention but would have to be analysed in conjunction with the rest of the Plusiina.

There are numerous biological topics that could employ plusiines as subjects. Perhaps the most important, as with all other groups of Lepidoptera, is the elucidation of life histories, to open up the possibilities for employing early stages in systematic analyses. The plusiines also lend themselves to questions of insect/plant interactions (How and why did *Abrostola asclepiadis* switch from *Urtica* to *Vincetoxicum*? Why does one *Lophoplusia* feed on a scentless mint and another on a tree lobelia with sticky, milky latex?); of pheromone biology (What *does Mouralia*

do with its giant hairpencil? Why do *Loboplusia* and *Chrysodeixis* have such elaborate scent organs?); and of biogeography (*Chrysodeixis* and *Autoplusia* are the prime candidates). If nothing else, I hope that this study will stimulate interest in the group so that such problems will be investigated. The Plusiinae could be much more than gold spots and burnished brasses, spectacles and silver Ys.

Addenda: notes added in proof

Taxa examined

Brachionycha sphinx Hufnagel was inadvertently used as the exemplar species for this genus instead of the type species, *B. nubeculosa* Esper.

Clade analysis

The larva of *Abrostola triopus* Hampson has been recorded feeding on *Commelina* sp. and the grass, *Pennisetum purpureum* (Sevastopulo, 1976). The former record is of particular interest as *Commelina* belongs to the same family (Commelinaceae) as the larval foodplants of *Mouralia*, the sister-genus of *Abrostola*. *A. triopus* is found in South Africa (with three doubtful records from Ethiopia and Kenya, probably misidentifications) and thus may be a critical species in the future understanding of the evolution of the Abrostolini.

Sevastopulo (1976) also recorded the larva of *Trichoplusia vittata* (as *transfixa*) feeding on *Artemisia africana*, so corroborating the hypothesised oligophagy of this group.

The larval foodplant of *Plusiopalpa dichora* (as *P. adrasta*) was given by Sevastopulo (1976) as *Coleus* (Lamiaceae).

An undescribed species of *Euchalcia* with yellow hindwings has recently been discovered in north-western Canada (J. D. Lafontaine, pers. comm.).

Polychrysia morigera appears to be extending its range eastwards in the U.S.A. (Covell & Medley, 1986). It was recorded from Kentucky in 1976, from Pennsylvania (recent unknown date) and was caught for the first time in Tennessee in 1984, trapped in the flowers of a Lady's Slipper Orchid (*Cypripedium kentuckiense*)!

Lafontaine (in press) has recently shown that there has been a considerable degree of confusion regarding the correct identity of *Syngrapha ottolenguii*. The type is a female that has had the abdomen of a male *Autographa californica* glued on. Examination of true *ottolenguii* has shown the species to be closely related to *S.* (*Palaeographa*) *interrogationis* and *S.* (*P.*) *nyiwonis*. Thus, *S. ottolenguii* almost certainly belongs in the subgenus *Palaeographa* of *Syngrapha*. In addition, the series examined by Eichlin & Cunningham (1978) was apparently mixed. When sorted correctly, *S. ottolenguii* was found to be endemic to Attu Island in the Aleutian Islands. '*S. ottolenguii*' in Alaska and Canada was shown by Lafontaine (in press) to be *Autographa buraetica* Staudinger, a species previously known only from the eastern Palaearctic and, until recently, considered as a subspecies or even a form of *Autographa pulchrina*.

Lafontaine (in press) has also examined a large number of specimens of *Syngrapha devergens* and *S. alticola*. He concluded that the genitalic differences noted by McDunnough (1944) are constant and that the Nearctic *S. alticola* should be reinstated as a species separate from the Palaearctic *S. devergens*.

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Appendix 1 Genera and type species of Plusiinae and outgroups.

The following is a list of the numbers of each sex examined in the Plusiinae and the outgroups. *Shensiplusia* was scored from drawings published by Chou & Lu (1974), while *Desertoplusia* and *Pseudochalcia* were described too recently to be included in the main analysis (but see Consensus classification).

Abrostola Ochsenheimer 1816
triplasia Linnaeus 1758 2 ♂, 2 ♀ (Fig. 32)

Acanthoplusia Dufay 1970*b*
tarassota Hampson 1913 2 ♂, 2 ♀ (Fig. 53)
Adeva McDunnough, 1944
albavitta Ottolengui 1902 1 ♂, 1 ♀ (Fig. 71)
Agrapha Hübner [1821] 1816
ahenea Hübner [1821] 1816 2 ♂, 2 ♀ (Fig. 57)
Allagrapha Franclemont 1964
aerea Hübner [1803] 2 ♂, 2 ♀ (Fig. 75)
Anadevidia Kostrowicki 1961
peponis Fabricius 1775 2 ♂, 2 ♀ (Fig. 37)
Anagrapha McDunnough 1944
falcifera Kirby 1837 3 ♂, 2 ♀ (Fig. 86)
Antoculeora Ichinosé 1973
ornatissima Walker 1858 2 ♂, 2 ♀ (Fig. 79)
Argyrogramma Hübner 1823
verruca Fabricius 1794 3 ♂, 2 ♀ (Fig. 59)
Autographa Hübner [1821] 1816
bractea [Denis & Schiffermüller] 1775 2 ♂, 2 ♀ (Fig. 88)
gamma Linnaeus 1758 2 ♂, 2 ♀ (Fig. 87)
Autoplusia McDunnough 1944
egena Guenée 1852 3 ♂, 2 ♀ (Fig. 80)
Caloplusia Smith 1884
hochenwarthi Hochenwarth 1785 2 ♂, 2 ♀ (Fig. 95)
Chrysanympha Grote 1895
formosa Grote 1865 1 ♂, 1 ♀ (Fig. 63)
Chrysodeixis Hübner [1821] 1816
chalcites Esper 1789 4 ♂, 2 ♀ (Fig. 39)
Cornutiplusia Kostrowicki 1961
circumflexa Linnaeus 1767 2 ♂, 3 ♀ (Fig. 89)
Ctenoplusia Dufay 1970*a*
limbirena Guenée 1852 2 ♂, 2 ♀ (Fig. 54)
Dactyloplusia Chou & Lu 1979
impulsa Walker 1865 2 ♂, 4 ♀ (Fig. 50)
Diachrysia Hübner [1821] 1816
chryson Esper 1789 2 ♂, 2 ♀ (Fig. 84)
Eosphoropteryx Dyar 1902
thyatiroides Guenée 1852 2 ♂, 2 ♀ (Fig. 61)
Erythroplusia Ichinosé 1962*a*
rutulifrons Walker 1858 4 ♂, 2 ♀ (Fig. 73)
Euchalcia Hübner [1821] 1816
variabilis Piller 1783 2 ♂, 2 ♀ (Fig. 67)
Eutheiaplusia Dufay 1970*a*
pratti Kenrick 1917 1 ♂ (holotype), 1 ♀ (Fig. 52)
Lamprotes R.L. 1817
c-aureum Knoch 1781 2 ♂, 2 ♀ (Fig. 35)
Loboplusia Roepke 1941
vanderweelei Roepke 1941 2 ♂ (holotype (Fig. 74) and paratype), 1 ♀ (holotype *Autographa pokhara*)
Lophoplusia Zimmerman 1958
pterylota Meyrick 1904 2 ♂, 2 ♀ (Fig. 92)
Macdunnoughia Kostrowicki 1961
confusa Stephens 1850 7 ♂, 3 ♀ (Fig. 76)
Mouralia Walker 1858
tinctoides Guenée 1852 2 ♂, 2 ♀ (Fig. 33)
Omorphina Alphéraky 1892
aurantiaca Alphéraky 1892 1 ♂, 1 ♀ (Fig. 31)
Palaeographa Kljutshko 1984
interrogationis Linnaeus 1758 2 ♂, 2 ♀ (Fig. 93)
Panchrysia Hübner [1821] 1816
deaurata Esper 1787 2 ♂, 2 ♀ (Fig. 64)

Plusia Ochsenheimer 1816
festucae Linnaeus 1758 2 ♂, 2 ♀ (Fig. 90)
Plusidia Butler 1879
cheiranthi Tauscher 1809 2 ♂, 2 ♀ (Fig. 34)
Plusiopalpa Holland 1894
dichora Holland 1894 1 ♂, 2 ♀ (Fig. 58)
Plusiotricha Holland 1894
livida Holland 1894 1 ♂
Polychrysia Hübner [1821] 1816
moneta Fabricius 1787 2 ♂, 2 ♀ (Fig. 62)
Pseudeva Hampson 1913
purpurigera Walker 1858 2 ♂, 2 ♀ (Fig. 36)
Pseudoplusia McDunnough 1944
includens Walker 1857 4 ♂, 2 ♀ (Fig. 38)
Puriplusia Chou & Lu 1974
purissima Butler 1878 2 ♂, 2 ♀ (Fig. 77)
Rachiplusia Hampson 1913
nu Guenée 1852 4 ♂, 2 ♀ (Fig. 72)
Sclerogenia Ichinosé 1973
jessica Butler 1878 3 ♂, 2 ♀ (Fig. 78)
Shensiplusia Chou & Lu 1974
nigribursa Chou & Lu 1974 [1 ♀]
Stigmoplusia Dufay 1970*a*
chalcoides Dufay 1968 1 ♂, 1 ♀ (Fig. 60)
Syngrapha Hübner [1821] 1816
devergens Hübner [1813] 2 ♂, 2 ♀ (Fig. 94)
Thysanoplusia Ichinosé 1973
intermixta Warren 1913 3 ♂, 2 ♀ (Fig. 47)
Trichoplusia McDunnough 1944
ni Hübner [1803] 3 ♂, 2 ♀ (Fig. 43)
Zonoplusia Chou & Lu 1979
ochreata Walker 1865 3 ♂, 2 ♀ (Fig. 49)

Plusiine taxa described too recently for inclusion in the analysis
Desertoplusia Kljutshko 1985
bella Christoph 1887 (Fig. 70)
Pseudochalcia Kljutshko 1985
inconspicua Graeser 1892 (Fig. 69)

Outgroups (nominal subfamily given in parentheses)
Anuga Guenée, 1852
constricta Guenée 1852 (Euteliinae) 2 ♂, 2 ♀ (Fig. 101)
Brachionycha Hübner [1819] 1816
sphinx Hufnagel 1766 (Cuculliinae) 2 ♂, 2 ♀ (Fig. 106)
Calophasia Stephens 1829 [June]
lunula Hufnagel 1766 (Cuculliinae) 2 ♂, 2 ♀ (Fig. 104)
Chalcopasta Hampson 1908
territans Edwards 1884 (Amphipyrinae) 2 ♂, 2 ♀ (Fig. 102)
Cucullia Schrank 1802
umbratica Linnaeus 1758 (Cuculliinae) 2 ♂, 2 ♀ (Fig. 105)
Diloba Boisduval 1840
caeruleocephala Linnaeus 1758 (Dilobidae) 2 ♂, 2 ♀ (Fig. 107)
Lophoptera Guenée 1852
squammigera Guenée 1852 (Stictopterinae) 2 ♂, 3 ♀ (Fig. 99)
Magusa Walker 1857
orbifera Walker 1857 (Amphipyrinae) 2 ♂, 2 ♀ (Fig. 97)
Oncocnemis Lederer 1853
confusa Freyer [1840] (Cuculliinae) 2 ♂, 2 ♀ (Fig. 103)

Paectes Hübner 1818
cristatrix Guenée 1852 (Euteliinae) 3 ♂, 2 ♀ (Fig. 100)
Stictoptera Guenée 1852
cucullioides Guenée 1852 (Stictopterinae) 2 ♂, 4 ♀ (Fig. 98)

Appendix 2 Plusiine generic-level taxa not employed in this study.

Cerviplusia Chou & Lu 1974. Type species: *Cerviplusia wukongensis* Chou & Lu 1974. *C. wukongensis* was synonymized with *Antoculeora ornatissima* (as *Macdunnoughia ornatissima*) by Dufay (1977). Thus, *Cerviplusia* is a junior subjective synonym of *Antoculeora* Ichinosé.

Chrysaspidia Hübner [1821] 1816. A junior objective synonym of *Plusia* Ochsenheimer.

Chrysoptera Berthold 1827. A junior objective synonym of *Lamprotes* R.L.

Cubena Walker 1856. Type species: *Phalaena polydamia* Stoll 1782. *C. polydamia* is a junior subjective synonym of *Lamprotes c-aureum* and has been treated as such for about a century. *Cubena* is thus a junior subjective synonym of *Lamprotes*.

Inguridia Butler 1879. Type species: *Inguridia abrostolina* Butler 1879. A junior subjective synonym of *Abrostola* Ochsenheimer. There is no doubt that *abrostolina* is congeneric with *Abrostola triplasia* and as far as I am aware, *Inguridia* has not been used this century.

Melanoplusia Chou & Lu 1978. A junior objective synonym of *Sclerogenia* Ichinosé.

Neoplusia Okano 1963. Type species: *Neoplusia furahatai* Okano 1963. *N. furahatai* was synonymized with *Chrysodeixis acuta* Walker by Dufay (1965), based on an examination of the genitalia. *Neoplusia* is thus a junior subjective synonym of *Chrysodeixis* Hübner and has been treated as such since 1965.

Palaeoplusia Hampson 1913. Type species: *Plusia venusta* Walker 1865. McDunnough (1944) considered *P. venusta* to be congeneric with *Plusia festucae* (as *Chrysaspidia festucae*). He therefore synonymized *Palaeoplusia* with *Chrysaspidia* and thus the former became a junior subjective synonym of *Plusia* Ochsenheimer. This decision has been upheld since and is followed in this study.

Paraplusia Mukerji & Krishnamorthy 1955. Type species: *Plusia confusa* Stephens 1850. This name is not nomenclaturally available because it was published after 1930 without a statement of characters differentiating the taxon.

Perloplusia Chou & Lu 1978. Type species: *Perloplusia pseudopyropia* Chou & Lu 1978. Chou & Lu (1979*a*) subsequently considered this species to be synonymous with *Erythroplusia pyropia* Butler and thus, by implication, *Perloplusia* is a junior subjective synonym of *Erythroplusia* (**syn. n.**).

Podioplusia Ichinosé 1962*a*. A junior objective synonym of *Anadevidia* Kostrowicki.

Scleroplusia Ichinosé 1962*a*. A junior objective synonym of *Macdunnoughia* Kostrowicki.

Unca Oken 1815. Included in a work rejected for nomenclatural purposes (ICZN, 1956).

Unca Lhomme [1929]. A junior objective synonym of *Abrostola* Ochsenheimer.

Yerongponga Lucas 1901. Type species: *Yerongponga exequialis* Lucas 1901. This genus and species was described in the Plusidae [sic] at a time when Plusidae referred to the quadrifine noctuids in general (Kitching, 1984). *Yerongponga* then, by inertia, became included in the Plusiinae (Nye, 1975). The species was not examined in this study (the type specimen could not be located; it was searched for, but not found, in the National Insect Collection, CSIRO, Canberra and in the South Australia Museum, Adelaide). However, from the description, the species is evidently much larger than any known plusiine and is most likely to be a species of *Platyja* Hübner (J. D. Holloway, pers. comm.). Thus *Yerongponga* can be transferred to the Catocalinae.

Appendix 3 Data matrix

Data set, characters 1–70, Plusiinae.

Omorphina	00000	01000	00101	00100	01010	01110	10000	00000	01000	0***0	01000	10010	00000	01000
Abrostola	11000	00001	00101	00101	02000	01010	10000	00000	00000	0**10	10000	10100	00000	01000
Mouralia	11000	00001	00122	00211	01000	01010	10000	00000	00000	0**10	10000	10100	00030	01000
Anadevidia	00010	00001	00111	00001	01000	01010	10000	00000	00000	0**10	00000	10110	00000	01000
Dactyloplusia	00110	10001	01121	00001	01000	01010	10000	00000	00000	0**10	00000	10111	00000	01000
Pseudoplusia	00110	10001	11121	00001	01000	01010	10000	00000	00000	0**10	00000	10100	00000	01000
Chrysodeixis	00110	10001	10121	00001	01000	01010	10000	00000	00000	0**10	00000	10110	00000	01000
Zonoplusia	00100	10001	01121	00001	01000	01010	10000	00000	00000	0**10	00000	10000	00000	01000
Trichoplusia	00110	10001	01121	00001	01000	01010	10000	00000	00000	0**10	00000	10101	00000	01000
Thysanoplusia	00010	10011	01121	00001	01000	01010	10000	00000	00000	0**10	00000	10101	00000	01000
Plusiotricha	00110	10001	101*1	00001	01000	01010	10000	00000	00000	0**10	00000	10102	10000	01000
Eutheiaplusia	00100	10001	00121	00001	01000	01010	10000	00000	00000	0**10	00000	10100	00000	01000
Agrapha	00110	00001	01121	00001	01000	01010	10000	00000	00000	0**10	00000	10100	00000	01000
Acanthoplusia	00120	10001	00121	00001	01000	01010	10000	00000	00000	0**10	00000	10101	00000	01000
Ctenoplusia	00130	10001	00121	00001	01000	01010	10000	00000	00000	0**10	00000	10102	00000	01000
Plusiopalpa	00110	10001	01121	00001	01000	01010	10000	00000	10000	0**10	00000	10100	10000	01000
Argyrogramma	00110	10001	00121	00001	01000	01010	10000	00000	00000	0**10	00000	10103	30000	01000
Stigmoplusia	00110	10001	10121	00001	01000	01010	10000	00000	00000	0**10	00000	10103	20000	01000
Shensiplusia	001**	*0001	*11*1	*0**1	01000	01010	10000	000*0	00000	0**10	00000	10***	*****	01000
Eosphoropteryx	00110	10001	00101	00101	01000	01010	10000	00010	00000	0**10	00000	10*10	00000	01000
Polychrysia	00111	10001	00101	00101	01000	01010	10000	00010	10000	0**11	00000	10110	00002	01000
Panchrysia	00010	10001	00101	10111	01000	01010	10000	00010	01000	0**10	00000	10110	00003	01000
Chrysanympha	00011	10001	00101	00101	01000	01010	10000	00010	11000	0**10	00000	10*10	00000	01000
Euchalcia	00040	00001	00101	00101	01000	01010	10000	00000	00000	0**10	00000	10010	00000	01000
Adeva	00041	00001	00101	00101	01000	01010	10000	00000	00000	0**10	00000	10*00	00000	01000
Plusidia	00010	00001	00101	00101	01000	01010	10000	00010	00000	0**10	00000	10010	00000	01000
Lamprotes	00110	10001	00101	10111	01000	01010	10000	00010	11000	0**10	00000	10110	00000	01000
Pseudeva	00011	10001	00101	10111	01000	01010	10000	00010	11000	0**11	00000	10110	00000	01000
Rachiplusia	00110	10001	00121	00001	01000	01010	10000	00000	00000	0**10	00000	10100	00120	01000
Erythroplusia	00111	00001	00101	00101	01000	01010	10000	00000	00000	0**10	00000	10110	00000	01000
Allagrapha	00010	10001	00101	10101	01000	01010	10000	00000	00000	0**10	00000	10010	00000	01000
Macdunnoughia	00110	10001	00101	00001	01000	01010	10000	00000	00000	0**10	00000	10110	00000	01000
Puriplusia	00110	10001	00101	00001	01000	01010	10000	00000	00000	0**10	00000	10110	00000	01000
Loboplusia	00110	00001	01101	00001	01000	01010	10000	00000	00000	0**10	00000	10100	00000	01000
Sclerogenia	00110	10001	01101	00001	01000	01010	10000	00000	00000	0**10	00000	10100	00000	01000
Autoplusia	00110	10001	00121	00001	01000	01010	10000	00000	00000	0**10	00000	10110	00010	01000
Antoculeora	00110	10001	01101	00101	01000	01010	10000	00000	00000	0**10	00000	10100	00000	01000
Diachrysia	00010	10011	00101	10101	01000	01010	10000	00000	00000	0**10	00000	10010	00001	01000
Anagrapha	00110	10001	00101	00101	01000	01010	10000	00000	00000	0**10	00000	10110	00020	01000
Autographa gamma	00110	10001	01101	00001	01000	01010	10000	00000	00000	0**10	00000	10110	00000	01000
A. bractea	00110	10001	00101	00101	01000	01010	10000	00000	00000	0**10	00000	10110	00000	01000
Cornutiplusia	00110	00001	01101	00101	01000	01010	10000	00000	00000	0**10	00000	10110	00010	01000
Plusia	00110	00001	00101	00101	01000	01010	10000	00000	00000	0**10	00000	10010	00000	01000
Lophoplusia	00110	00001	01101	00001	01000	01010	10000	00000	00000	21110	00000	10100	00003	01000
Palaeographa	00110	10001	01101	00101	01000	01010	10000	00000	00000	0**10	00000	10100	00010	01000
Syngrapha	00110	01001	01101	00101	01010	01010	10000	00000	00000	0**10	00000	10100	00010	01000
Caloplusia	00110	01001	01101	00101	01010	01010	10000	00000	00000	0**10	00000	10110	00220	01000

Data set, characters 71–150, Plusiinae.

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Omorphin 00000 00**0 ***** ***** ***** 00000 00000 00000 00000 00100 00000 01001 10000 01000 00310 *1100

Abrostol 00100 00**1 **0** ***0* 00000 00011 01100 01000 00000 001*0 2*011 1000* 0*010 00000 001** 00100
Mouralia 00100 00**1 **500 00000 00000 00011 01100 01000 00000 00100 00011 1000* 0*010 10000 0020* 00100

Anadev   00200 00**1 **300 00010 00000 00010 00001 10100 00000 10100 00000 00001 10000 10000 00310 000**
Dactylo  00200 11102 **200 00010 11120 00010 00001 10000 00000 00100 00000 00101 10000 10000 00310 00110
Pseudo   00200 10**1 **0** ****0 00000 00010 00001 10001 10000 00101 00000 00200 10000 10000 00300 00100
Chryso   00200 13001 **500 00010 10110 01010 00000 10001 10000 00101 00000 01100 10000 10000 00300 00100
Zono     00200 10**1 **200 00010 10020 00010 00000 10101 00000 00100 00000 00001 10000 10000 00310 00100
Tricho   00200 11002 **310 00010 11220 00010 00001 10100 00000 00100 00000 0000* 0*000 10000 00300 00110
Thysano  00200 11002 **300 00010 11120 00010 00000 10101 01000 00100 00000 00101 10000 10000 00300 00100
P'tricha 00200 12002 **210 00010 21220 00010 00000 10001 03000 00110 00000 0*001 10100 10101 00320 00100
Eutheia  00200 12002 **0** ***10 ****0 00010 00000 10001 00000 00100 00000 0*001 10000 10101 00310 00100
Agrapha  00200 12012 **210 11110 21220 00110 00001 10101 01000 00100 00000 00000 10000 10100 00320 00110
Acantho  00200 11002 **300 11010 23220 00010 00000 10001 01000 00110 00000 00001 10100 10100 00300 00100
Cteno    00200 11202 **210 01010 23220 00010 00000 10101 01000 00110 00000 00001 10100 10100 00300 00100
P'palpa  00200 12002 **400 00010 13220 00010 00000 10101 01000 00100 00000 00101 10000 10000 00300 00100
Argyro   00200 12332 **411 10111 22330 00110 00001 10001 01000 00100 20000 00000 10000 10000 00300 00100
Stigmo   00200 12022 **311 10011 22330 01010 00000 10101 12000 00100 00000 00000 10000 10*00 00310 00100
Shensi   00200 ***** ***** ***** ***** ***** ***** ***** ***** ***** ***** ***** ***** ***** ***** *****

Eosphor  00200 00**1 **0** ***0* 00000 00010 10000 10000 00000 01100 10000 01001 10000 00000 00300 00100
Polychry 00200 00**1 **0** ***0* 00000 00010 10000 10010 00000 01100 10000 01001 10000 00000 00300 *1100
Panchry  00200 00**1 **0** ***0* 00000 00010 10000 10010 00000 01100 10000 01001 11000 00000 00300 *1100
Chrysan  00200 00**1 **0** ***0* 00000 00010 10000 11010 00000 01100 10000 01001 11000 00000 00300 *1100
Euchalc  00200 00**1 **0** ***0* 00000 00010 10000 10010 00000 01100 10000 01001 10000 00000 00310 *1100
Adeva    00200 00**1 **0** ***0* 00000 00010 10000 10010 00000 01100 10000 01001 10000 00000 00310 *1100
Plusid   00200 00**1 **0** ***0* 00000 00010 10000 10010 00000 01100 10000 01001 10000 00000 00320 *1100
Lamprot  00200 00**1 **0** ***0* 00000 00010 10000 10010 00000 01100 10000 01001 10000 00000 00310 *1100
Pseudev  00200 00**1 **0** ***0* 00000 00010 10000 10010 00000 01100 10000 01001 10000 00000 00320 *1100

Rachi    00200 00**1 **300 00000 00000 00010 00000 10001 00010 11100 10000 01001 10000 00010 00300 000**
Erythro  00200 00**1 **200 00000 00001 00010 00010 10100 00000 11100 10000 01001 10000 00000 10301 001**
Alla     00200 00**1 **200 00000 00001 00020 00000 10000 00100 11100 10000 00001 10000 01010 11300 00100
Macdunn  00200 00**1 **200 00000 00001 00020 00000 10000 00100 11100 10000 01001 10000 01010 11301 00102
Puri     00200 00**1 **200 00000 00001 00020 00000 10000 00100 11100 10000 01001 10000 01010 11301 00101
Lobo     00200 0***1 **200 0**00 00001 00010 *000* 10000 00100 *1100 100** 0**01 10000 000*0 00310 000**
Sclero   00200 00**1 **200 00000 00000 00010 00000 10100 00000 11100 10000 01001 10000 00000 12300 000**
Autoplus 00200 00**1 **300 00000 00001 00010 00000 10000 00000 11100 10000 0100* 0*000 00000 02300 000**
Antocul  00200 00**1 **200 00000 00001 00010 00010 10000 00000 00200 10000 01001 10000 00*0* 12301 000**

Diachry  00200 00**1 **100 00000 00000 00010 00000 10000 00000 11100 10000 01001 10000 00000 00300 1*100
Anagraph 00200 00**1 **100 00000 00000 00010 00001 10000 00100 11100 10000 02001 10000 00000 00210 1*100
A.gamma  00200 00**1 **100 00000 00000 00010 00001 10110 00000 11100 10000 01001 10000 00000 00300 1*100
A.bract  00200 00**1 **100 00000 00000 00010 00001 10110 00000 11100 10000 01001 10000 00000 00300 1*100
Cornuti  00200 00**1 **100 00000 00000 00010 00001 10110 00000 11100 10000 01001 10000 00000 00300 1*100
Plusia   00200 00**1 **300 00000 00000 00010 00000 10110 00000 11100 10000 01001 10000 00000 00300 1*100
Lopho    00200 00**1 **100 00000 00000 00010 00001 11110 00000 11100 10000 01001 10000 00000 00320 1*100
Palaeo   00200 00**1 **100 00000 00000 01010 00001 10110 00000 11100 10000 02001 10000 00000 00310 1*110
Syngraph 00200 00**1 **0** ***0* 00000 01010 00001 10110 00000 11100 10000 03001 10000 00000 00310 1*110
Caloplus 00200 00**1 **100 00000 00000 01010 00001 10110 00000 11100 10000 03001 10000 00000 00310 1*110
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Data set, characters 151–216, Plusiinae.

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Mouralia 00000 01000 00*** *0011 00000 00100 01000 01100 10000 00000 00000 00000 00000 0

Anadev   00000 02200 01000 00000 00**0 00100 01010 00000 00000 00000 00000 00010 00000 0
Dactylo  00000 02200 00*** *1000 01110 00100 01011 00000 00000 00000 00000 00010 00000 0
Pseudo   00000 02200 00*** *1000 01110 00100 01011 00000 00000 10000 00000 00000 00010 0
Chryso   00000 02200 00*** *1000 00110 00100 01011 00000 00000 10000 00000 01010 00000 0
Zono     00000 02200 01000 01000 00100 00100 01011 00000 00000 00000 00110 00010 00000 0
Tricho   00000 02200 01000 01000 00100 00100 01011 00000 00000 00000 00211 00000 00000 0
Thysano  00000 02210 01000 01000 00100 00100 01011 00000 00000 00000 00110 00000 00000 0
P'tricha 00000 02211 00*** *1000 00100 **1** ***** ***** ***** ***** ***** ***** ***** *
Eutheia  00000 02211 00*** *1000 00100 00100 01011 00000 00000 00000 00111 00010 00000 0
Agrapha  00000 02200 01000 01000 00100 00100 01011 00000 00000 10000 00000 01000 00010 0
Acantho  00000 02200 00*** *1000 00100 00100 01011 00000 00000 01000 00000 00000 00000 0
Cteno    00000 02200 00*** *1000 00100 00100 01011 00000 00000 01000 00000 00000 00010 0
P'palpa  00000 02200 00*** *1000 00100 00100 01011 00000 00000 00000 10000 00000 00210 0
Argyro   00000 02200 01000 01000 00100 00100 01011 00000 00000 00000 00000 00000 00010 0
Stigmo   00000 02200 01000 01000 00100 00100 01011 00000 00000 00000 00000 00000 00000 0
Shensi   ***** ***** ***** ***** ***** ***00 010** *0000 0*000 10*00 001*0 000*0 000*0 *

Eosphor  00000 02100 00*** *0000 00001 00200 01010 00000 00000 00000 00000 00000 00100 0
Polychry 00000 02100 01001 00000 00000 00200 01010 00000 00000 10000 00000 00000 00000 0
Panchry  00010 02100 01100 00000 00**0 00200 01110 00000 00000 10000 00000 00010 00000 0
Chrysan  00010 02100 01100 00000 00**0 00200 01110 00000 00000 10000 00000 00000 00000 0
Euchalc  00010 02100 01010 00100 00000 00200 01010 00000 00000 10000 10001 00000 00000 0
Adeva    00010 02100 01010 00100 00000 00200 01110 00000 00000 10000 00001 00000 00000 0
Plusid   00000 02100 01000 00100 10**0 00200 01110 10000 00020 10000 00001 00000 00000 0
Lamprot  00000 02100 00*** *0100 10**0 00200 01110 10000 10010 10000 10000 00000 00000 0
Pseudev  00000 02100 01000 00100 10**0 00200 01110 10000 00020 10000 00000 00000 00000 0

Rachi    00010 02100 01000 00000 00000 00100 01010 00000 10000 00300 00000 10000 00200 1
Erythro  00001 02200 00*** *0000 00**0 00100 01010 00010 00100 00000 00000 00010 00000 0
Alla     00000 02100 00*** *0000 00000 11100 01010 00010 10100 00000 10000 00000 00200 0
Macdunn  00000 02200 00*** *0000 00**1 11100 01010 00010 11100 00000 00000 10000 00300 0
Puri     00000 02100 00*** *0000 00000 10100 01010 00010 12100 00000 00000 10010 00300 0
Lobo     0000* 02100 00*** *0*0* 00**1 01*00 010*0 00010 *0100 00000 00000 00010 00200 0
Sclero   00001 02100 00*** *0000 00000 11100 01010 00010 00100 00100 00000 00000 01300 0
Autoplus 00000 02000 00*** *0000 00000 11100 01010 00010 00100 00211 00000 00000 01300 1
Antocul  00000 02000 00*** *0000 00000 11100 01010 00000 10100 00211 00000 00000 01300 0

Diachry  00000 02100 01001 00000 00000 00100 01010 00000 10000 00000 00000 00000 00000 0
Anagraph 00000 02100 01000 00000 00000 00100 01010 00010 00000 00000 00000 00000 00000 0
A.gamma  00000 02100 01000 00000 00000 00100 01010 00000 00000 00000 00000 00000 00000 0
A.bract  00000 02100 01000 00000 00**0 00100 01010 00000 00000 00000 00000 00000 00002 0
Cornuti  00000 02100 01000 00000 00**0 00100 01010 00000 00000 00000 00000 00000 00003 0
Plusia   00000 02100 01000 10000 00000 00100 01010 00000 00000 00000 00000 00000 00001 0
Lopho    00000 02100 01000 20000 00000 00100 01010 00000 00000 00000 00000 00000 00001 0
Palaeo   00000 02100 00*** *0000 00000 00100 01010 00010 10000 00000 10000 00000 00000 0
Syngraph 00000 02100 00*** *0000 00000 00100 01010 00010 10000 00000 10000 00000 00000 0
Caloplus 00000 02100 00*** *0000 00**0 00100 01010 00010 10000 00000 10000 00000 00000 0
```

Data set, characters 1–70, 71–140, 141–210, 211–216, outgroups.

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Magusa          00000 00000 00102 00312 00100 10100 21111 01000 00000 0**00 00000 10*00 00000 01000
Stictoptera     10000 00100 00050 01002 00101 10101 21111 01000 00101 0**00 00100 11*00 12000 11101
Lophoptera      00000 00100 00050 01002 00101 10100 21111 01000 00100 0**00 02000 11000 12000 11001
Paectes         00000 00000 00040 00002 00101 10100 21212 11000 00101 10100 02000 11100 01000 11201
Anuga           10000 00000 00030 01002 00101 10101 21212 11000 00000 10100 02100 11100 01000 11201
Chalcopasta     00000 00011 00002 00201 00000 00100 21101 00001 00010 0**10 00000 00110 00000 01010
Oncocnemis      00000 00000 00102 00201 01000 00100 21101 00001 01010 0**00 00000 00000 00000 00010
Calophasia      00000 00000 00103 00311 01000 01100 20101 00100 00000 0**00 00010 00000 00000 01000
Cucullia        00000 00000 00102 00111 02000 00100 20001 00101 00000 0**00 00010 00*10 00000 01000
Brachionycha    00000 00000 00122 00100 10000 00100 02*2* 00101 00010 22000 00001 00000 00000 01010
Diloba          00000 00000 00161 00000 12000 02100 02*2* 00101 00000 22000 00001 00*00 00000 00000

Magusa          00001 00**3 21*** ***** ***** 00000 00000 0100* 00000 00000 00000 0000* 0*001 00000
Stictoptera     01300 00**3 02*** ***** ***** 00000 00000 0100* 000*0 0***0 10100 000** 0*000 00000
Lophoptera      00300 00**3 01*** ***** ***** 00000 00000 01000 00010 0***0 10100 0000* 0*000 00000
Paectes         11310 00**3 01*** ***** ***** 1***0 0**00 *0001 00011 00*00 01100 0001* 0*000 00000
Anuga           11310 00**3 1**** ***** ***** 2***0 0**00 *0000 00011 0**00 01100 0001* 0*000 00000
Chalcopasta     00000 00**0 ***** ***** ***** 01000 00001 10000 00000 00100 00000 0000* 0*001 00000
Oncocnemis      00000 00**0 ***** ***** ***** 00000 00000 00000 00000 001*0 3*000 0000* 0*001 00000
Calophasia      00000 00**3 30*** ***** ***** 1***0 0**00 00000 00000 000*0 3*000 0000* 0*001 00000
Cucullia        00002 00**3 30*** ***** ***** 00000 00000 00010 00000 00100 00000 0010* 0*001 00000
Brachionycha    10000 00**0 ***** ***** ***** 1***0 0**00 00000 00000 00100 00000 0000* 0*000 00000
Diloba          10000 00**0 ***** ***** ***** 1***0 0**00 00000 00000 0***0 **100 0000* 0*000 00000

Magusa          010** 00100 00000 10000 00*** *0000 00000 00000 00000 00000 00000 00000 00000 00001
Stictoptera     000** 000** 10100 11000 10*** **000 00000 00111 10*00 00000 00000 01000 00000 00002
Lophoptera      010** 00100 10100 11000 10*** **000 00000 00111 10*00 00001 00001 000*0 01000 00022
Paectes         000** 000** 011** 00000 10*** *0000 00000 00111 00*00 00001 00001 000*0 01000 00002
Anuga           000** 000** 011** 10000 10*** **000 00000 00111 00*00 00001 00001 000*0 01000 00002
Chalcopasta     001** 00100 00000 01000 00*** *0000 00000 00000 00000 00000 00000 10000 00000 00000
Oncocnemis      001** 00100 00000 01000 00*** *0000 00000 00000 00000 00000 00000 00000 00000 00010
Calophasia      010** 00100 00000 01000 00*** *0000 00000 00001 00000 00000 00000 00000 00000 00001
Cucullia        0020* 00100 00000 01000 00*** *0000 00000 00000 00000 00000 00000 10000 00001 00011
Brachionycha    000** 00100 00000 01000 00*** *0000 00000 10000 00000 00000 10000 00000 00000 00100
Diloba          100** 00100 00000 01000 00*** *0000 00000 00000 00000 00000 00020 10000 00000 00100

Magusa          00000 0
Stictoptera     10000 0
Lophoptera      20000 0
Paectes         10000 0
Anuga           00000 0
Chalcopasta     00200 0
Oncocnemis      00000 0
Calophasia      00003 0
Cucullia        00000 0
Brachionycha    00000 0
Diloba          00200 0
```

Appendix 4 New taxa and synonymy, status changes and revivals.

New taxa

Autoplusiina **subtrib. n.**

New combinations (previous generic combination given in parentheses, genus of original description given in square brackets).

Pseudoplusia dalei (Wollaston) (from *'Plusia' dalei*) [*Plusia*]
Agrapha meretricia (Schaus) (from *'Plusia' meretricia*) [*Plusia*]
Agrapha calceolaris (Walker) (from *'Plusia' calceolaris*) [*Plusia*]
Autographa camptosema (Hampson) (from *Macdunnoughia camptosema*) [*Phytometra*]
Autographa schalisema (Hampson) (from *Macdunnoughia schalisema*) [*Phytometra*]

New synonymy

Autographa emmetra Dufay, **syn. n.** of *A. schalisema* (Hampson)
Perloplusia Chou & Lu, **syn. n.** of *Erythroplusia* Ichinosé

Valid genera

Thysanoplusia **gen. rev.** (from synonymy with *Trichoplusia*)
Ctenoplusia **gen. rev.** (from synonymy with *Agrapha*)
Cornutiplusia **gen. rev.** (from synonymy with *Syngrapha*)
Lophoplusia **stat. n.** (from subgenus of *Plusia* s.l.)

Subgeneric changes

Pseudoplusia **stat. n.** – subgenus of *Chrysodeixis*
Eutheiaplusia **stat. n.** – subgenus of *Plusiotricha*
Acanthoplusia **stat. rev.** – subgenus of *Ctenoplusia*
Adeva **stat. n.** – subgenus of *Euchalcia*
Caloplusia **stat. n.** – subgenus of *Syngrapha*

Appendix 5 Generic classification of the Plusiinae

Subfamily Plusiinae
  Tribe Omorphinini
    Omorphina
  Tribe Abrostolini
    Abrostola
    Mouralia
  Tribe Argyrogrammatini
    Argyrogrammatini *incertae sedis*: *Shensiplusia*
    Anadevidia
    Chrysodeixis
      subgenus *Chrysodeixis*
      subgenus *Pseudoplusia* **stat. n.**
    Zonoplusia
    Argyrogramma-complex
      Trichoplusia, *sedis mutabilis*
      Thysanoplusia genus-group, *sedis mutabilis*
        Thysanoplusia **stat. rev.**
        Dactyloplusia
      Plusiotricha, *sedis mutabilis*
        subgenus *Plusiotricha*
        subgenus *Eutheiaplusia* **stat. n.**
      Ctenoplusia, *sedis mutabilis* **stat. rev.**
        subgenus *Ctenoplusia* **stat. rev.**
        subgenus *Acanthoplusia* **stat. rev.**
      Agrapha, *sedis mutabilis*
      Plusiopalpa, *sedis mutabilis*
      Argyrogramma genus-group, *sedis mutabilis*
        Argyrogramma
        Stigmoplusia

Tribe Plusiini
- Subtribe Euchalciina
  - Euchalciina *incertae sedis*: *Pseudochalcia*
  - *Eosphoropteryx*
  - *Polychrysia*
  - *Panchrysia* genus-group, *sedis mutabilis*
    - *Panchrysia*
    - *Chrysanympha*
  - *Euchalcia* genus-group, *sedis mutabilis*
    - *Desertoplusia*
    - *Euchalcia*
      - subgenus *Euchalcia*
      - subgenus *Adeva*
  - *Lamprotes* genus-group, *sedis mutabilis*
    - *Plusidia*
    - *Lamprotes*
    - *Pseudeva*
- Plusiini *incertae sedis*: *Diachrysia*
  Anagrapha
  Rachiplusia
- Subtribe Autoplusiina **subtrib. n.**
  - Autoplusiina *incertae sedis*: *Erythroplusia*
    Loboplusia
  - *Autoplusia* genus-group
    - *Sclerogenia*
    - *Autoplusia*
    - *Antoculeora*
  - *Macdunnoughia* genus-group
    - *Allagrapha*
    - *Macdunnoughia*
      - subgenus *Macdunnoughia*
      - subgenus *Puriplusia*
- Subtribe Plusiina
  - *Autographa*, *sedis mutabilis*
  - *Plusia*-complex, *sedis mutabilis*
    - *Plusia* genus-group
      - *Plusia*
      - *Lophoplusia* **stat. n.**
    - *Cornutiplusia* genus-group
      - *Cornutiplusia* **stat. rev.**
      - *"Autographa" bractea*
  - *Syngrapha*, *sedis mutabilis*
    - subgenus *Palaeographa*
    - subgenus *Syngrapha*
    - subgenus *Caloplusia* **stat. n.**

Figs 31–36 31, *Omorphina aurantiaca* (wingspan [ws] = 22 mm). 32, *Abrostola triplasia* (ws = 33 mm). 33, *Mouralia tinctoides* (ws = 45 mm). 34, *Plusidia cheiranthi* (ws = 30 mm). 35, *Lamprotes c-aureum* (ws = 33 mm). 36, *Pseudeva purpurigera* (ws = 32 mm). Wingspans for Figs 31–107 are measured from wingtip to wingtip and are given to the nearest mm.

Figs 37–42 37, *Anadevidia peponis* (ws = 41 mm). 38, *Chrysodeixis (Pseudoplusia) includens* (ws = 37 mm). 39, *Chrysodeixis (Chrysodeixis) chalcites* (ws = 38 mm). 40, *C. (C.) argentifera* (ws = 35 mm). 41, *C. (C.) illuminata* (ws = 39 mm). 42, *C. (C.) kebea* (ws = 34 mm).

Figs 43–48 43, *Trichoplusia ni* (ws = 35 mm). 44, *T. sestertia* (ws = 30 mm). 45, *T. exquisita* (ws = 35 mm). 46, *T. lectula* (ws = 30 mm). 47, *Thysanoplusia intermixta* (ws = 35 mm). 48, *Thy. daubei* (ws = 27 mm).

Figs. 49–54 49, *Zonoplusia ochreata* (ws = 25 mm). 50, *Dactyloplusia impulsa* (ws = 24 mm). 51, *Plusiotricha (Plusiotricha)* sp. near *livida* (ws = 31 mm). 52, *Plusiotricha (Eutheiaplusia) pratti* (ws = 36 mm). 53, *Ctenoplusia (Acanthoplusia) tarassota* (ws = 35 mm). 54, *Ctenoplusia (Ctenoplusia) limbirena* (ws = 34 mm).

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Figs 55–60 55, *Ctenoplusia (Ctenoplusia) euchroa* (ws = 41 mm). 56, *'Plusia'* (s.l.) *megaloba* (ws = 28 mm). 57, *Agrapha ahenea* (ws = 37 mm). Note the well developed dorso-lateral hair tufts. 58, *Plusiopalpa dichora* (ws = 43 mm). 59, *Argyrogramma verruca* (ws = 31 mm). 60, *Stigmoplusia chalcoides* (ws = 37 mm).

Figs 61–66 61, *Eosphoropteryx thyatiroides* (ws = 38 mm). 62, *Polychrysia moneta* (ws = 39 mm). Note the erect tegulae and scattered black scales on the forewing. 63, *Chrysanympha formosa* (ws = 33 mm). 64, *Panchrysia deaurata* (ws = 37 mm). 65, *P. v-argenteum* (ws = 35 mm). 66, *P. dives* (ws = 26 mm).

Figs 67–71 67, *Euchalcia (Euchalcia) variabilis* (ws = 38 mm). 68, *'Plusia' hampsoni* (ws = 34 mm). 69, *Pseudochalcia inconspicua* (ws = 35 mm). 70, *Desertoplusia bella* (ws = 28 mm). 71, *Euchalcia (Adeva) albavitta* (ws = 27 mm).

Figs 72–77 72, *Rachiplusia nu* (ws = 33 mm). 73, *Erythroplusia rutulifrons* (ws = 29 mm). 74, *Loboplusia vanderweelei* (holotype) (ws = 36 mm). Note the enlarged anal fold on the hindwing, the large dorsal hair tuft on the hindleg and the modified scales on the outer third of the hindwing. 75, *Allagrapha aerea* (ws = 40 mm). 76, *Macdunnoughia (Macdunnoughia) confusa* (ws = 36 mm). 77, *M. (Puriplusia) purissima* (ws = 32 mm).

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Figs 78–83 78, *Sclerogenia jessica* (ws = 30 mm). 79, *Antoculeora ornatissima* (ws = 37 mm). 80, *Autoplusia egena* (ws = 40 mm). 81, *A. olivacea* (ws = 43 mm). 82, *'Syngrapha' gammoides* ♂ (ws = 46 mm). 83, *'S.' gammoides* ♀ (ws = 44 mm). Note the sexual dimorphism in *'S.' gammoides*; the male is grey and more contrastingly patterned than the brown female.

Figs 84–89 84, *Diachrysia chryson* (ws = 40 mm). 85, *D. chrysitis* (ws = 36 mm). 86, *Anagrapha falcifera* (ws = 35 mm). 87, *Autographa gamma* (ws = 40 mm). 88, *'Autographa' bractea* (ws = 36 mm). 89, *Cornutiplusia circumflexa* (ws = 38 mm).

Figs 90–95 90, *Plusia festucae* (ws = 37 mm). 91, *P. venusta* (ws = 33 mm). 92, *Lophoplusia pterylota* (ws = 38 mm). Note the strongly bipectinate antennae. 93, *Syngrapha (Palaeographa) interrogationis* (ws = 33 mm). 94, *S. (Syngrapha) devergens* (ws = 28 mm). 95, *S. (Caloplusia) hochenwarthi* (ws = 28 mm).

Figs 96–101 96, *Syngrapha (Syngrapha) parilis* (ws = 26 mm). 97, *Magusa orbifera* (ws = 40 mm). 98, *Stictoptera cucullioides* (ws = 35 mm). Note the bulbous eyes. 99, *Lophoptera* sp. near *squammigera* (ws = 31 mm). 100, *Paectes cristatrix* (ws = 30 mm). Note the strongly bipectinate antennae. 101, *Anuga constricta* (ws = 36 mm). Note the very weakly bipectinate antennae.

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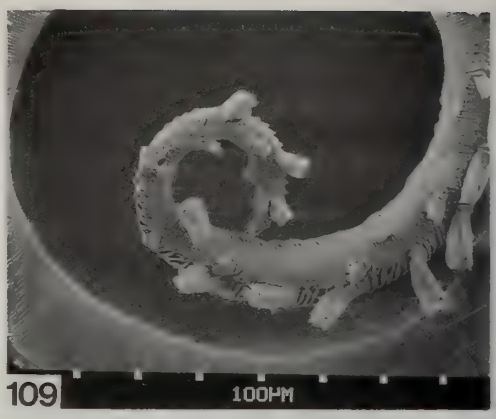
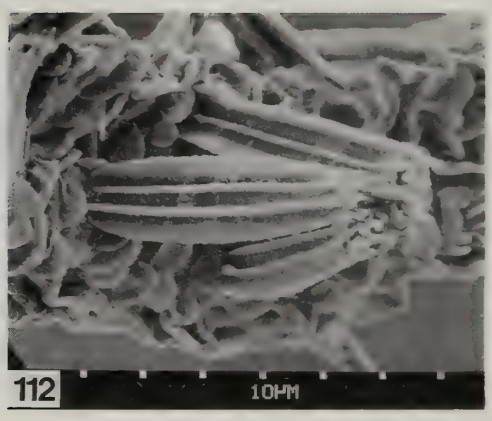
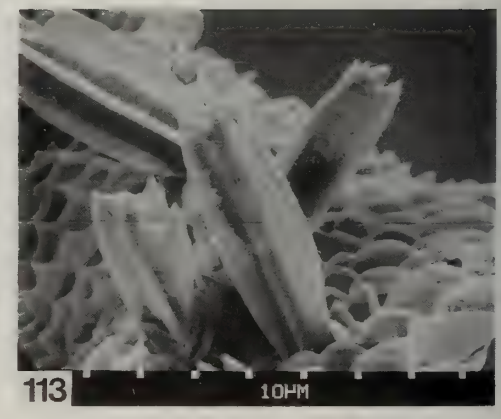
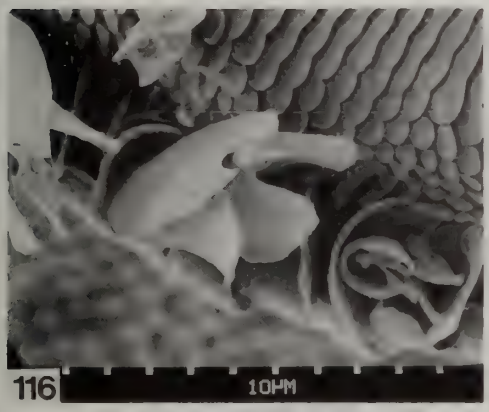
Figs 102–107 102, *Chalcopasta territans* (ws = 36 mm). 103, *Oncocnemis confusa* (ws = 28 mm). 104, *Calophasia lunula* (ws = 29 mm). 105, *Cucullia umbratica* (ws = 50 mm). 106, *Brachionycha sphinx* (ws = 41 mm). 107, *Diloba caeruleocephala* (ws = 37 mm).

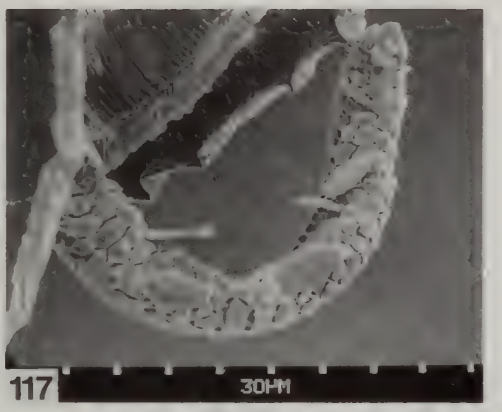


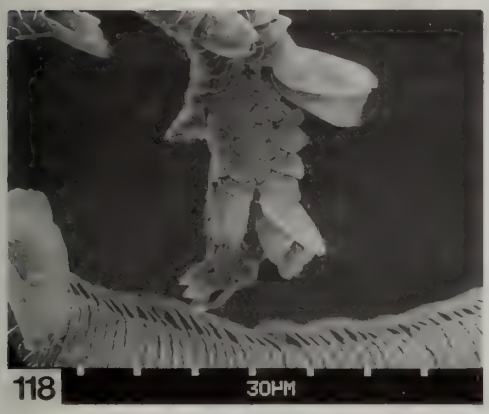


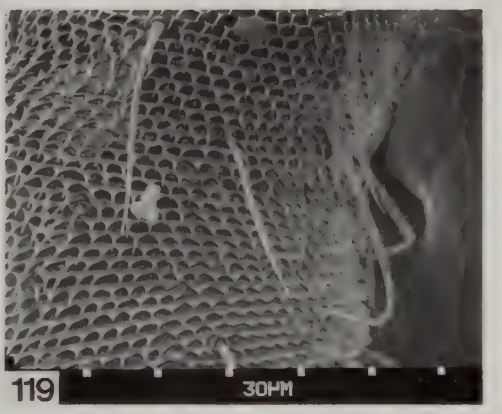


Figs 108–113 Probosces. 108, apex of proboscis, *Autographa bractea*. Note that the strengthening bars remain semicircular to the apex and that there are few apical sensilla. 109, apex of proboscis, *Anuga constricta*. Note that the strengthening bars break up apically into small plates and that there is a large number of apical sensilla. 110, styloconic sensillum, *Autographa bractea*. 111, styloconic sensillum, *Cucullia umbratica*. 112, styloconic sensilla, *Oncocnemis confusa*. Note the longitudinal ridges that are absent in *Autographa* and *Cucullia*. 113, styloconic sensilla, *Stictoptera cucullioides*. Note the three poorly developed ventral ridges. Scale as indicated.

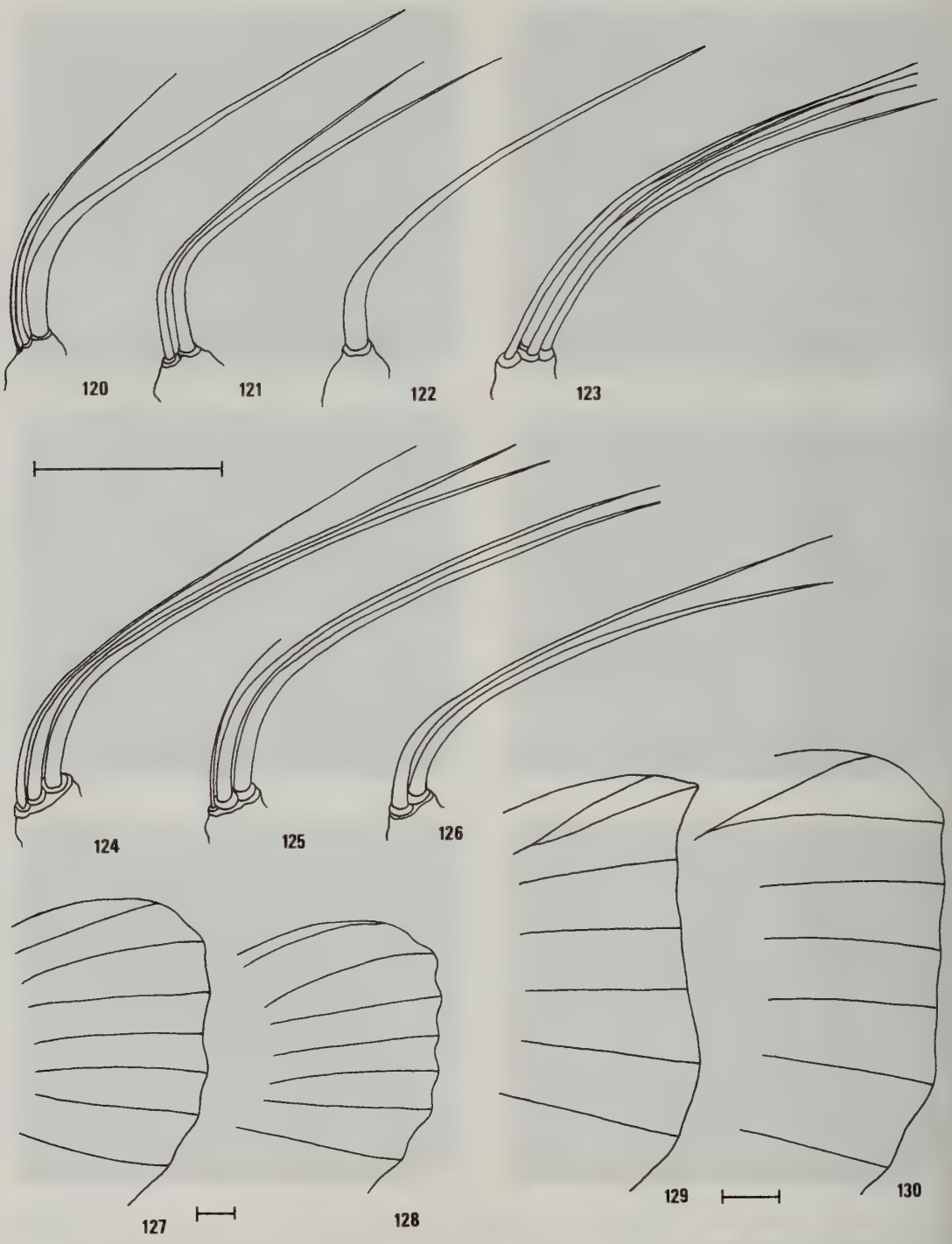




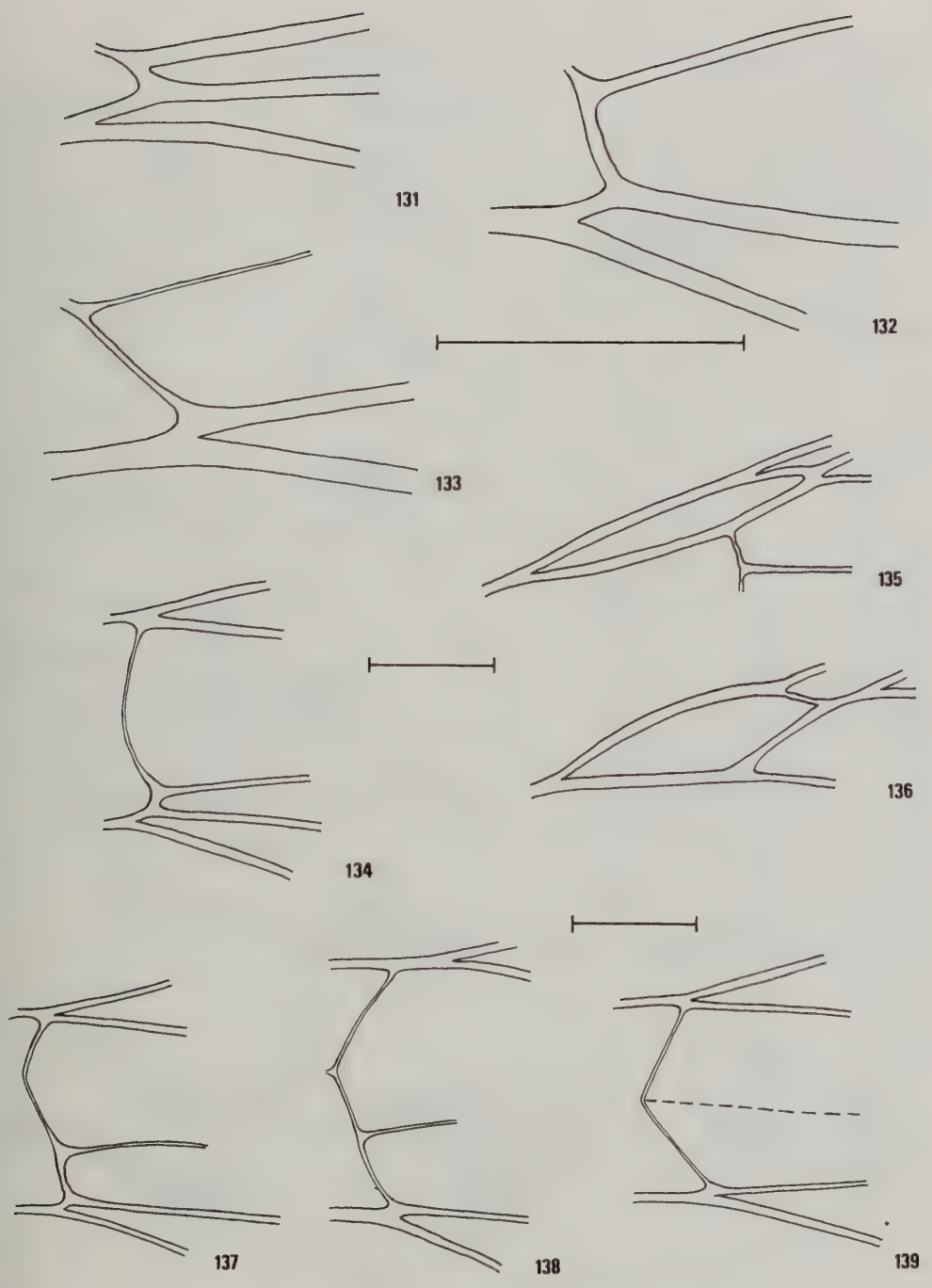




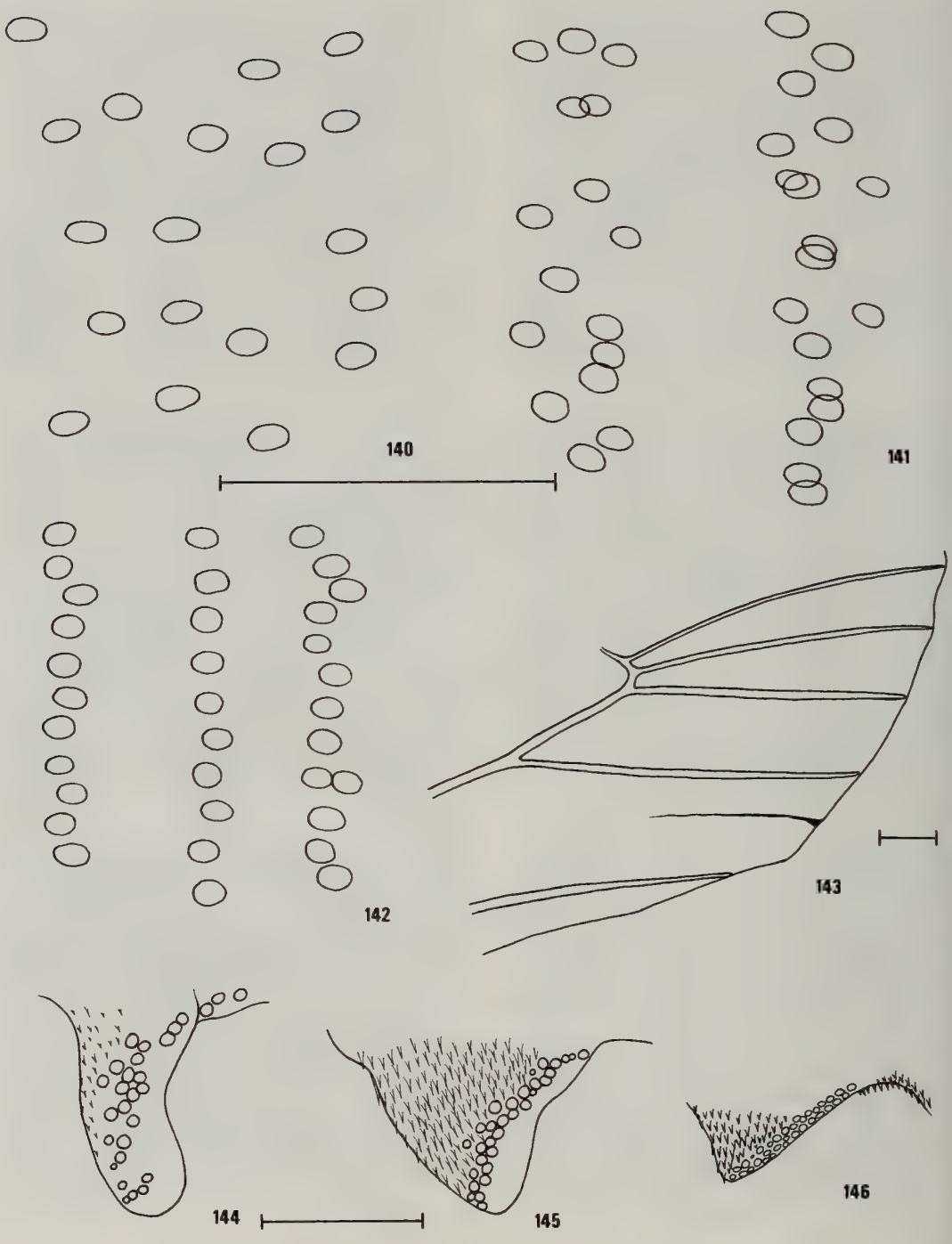
Figs 114–119 Probosces. 114, styloconic sensillum, *Paectes cristatrix*. 115, styloconic sensillum, *Anuga constricta*. 116, styloconic sensillum, *Paectes cristatrix*. Note on Figs 114–116, the three enlarged 'wings'. 117, apex of proboscis, *Cucullia umbratica*. Note that the strengthening bars are broken up apically into small nodules. 118, apex of proboscis, *Anuga constricta*. 119, base of proboscis, *Anuga constricta*. Note the regular arrangement of the microtrichia. Scale as indicated.



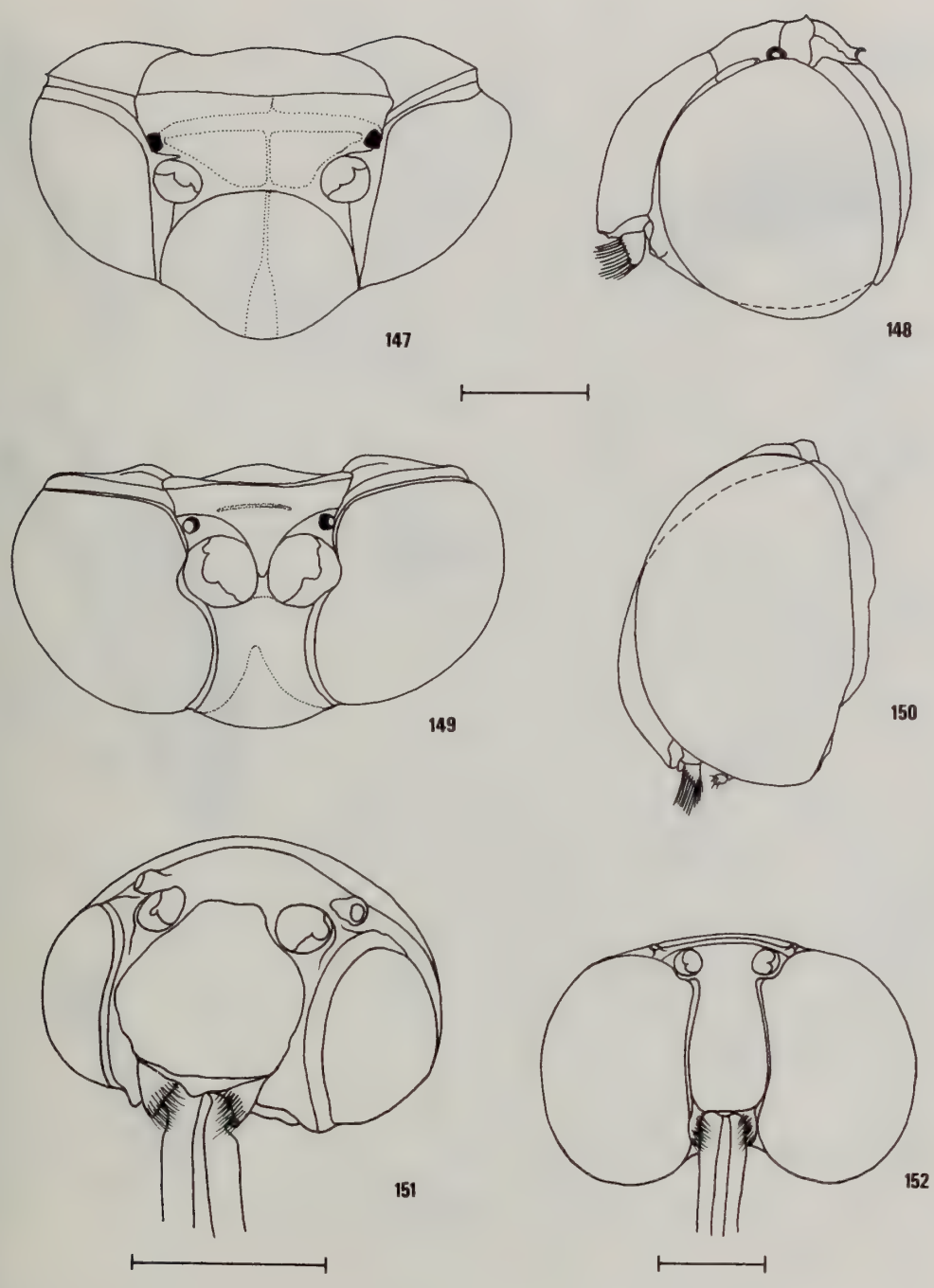
Figs 120–130 120–126, female frenula, right hindwings: (120) *Anuga*; (121) *Paectes*; (122) *Stictoptera*; (123) *Diloba*; (124) *Autographa gamma*; (125) *Anadevidia*; (126) *Thysanoplusia*. 127, 128, right hindwing apices: (127) *Lamprotes*; (128) *Allagrapha*. 129, 130, right forewing apices: (129) *Pseudeva*; (130) *Lophoplusia*.



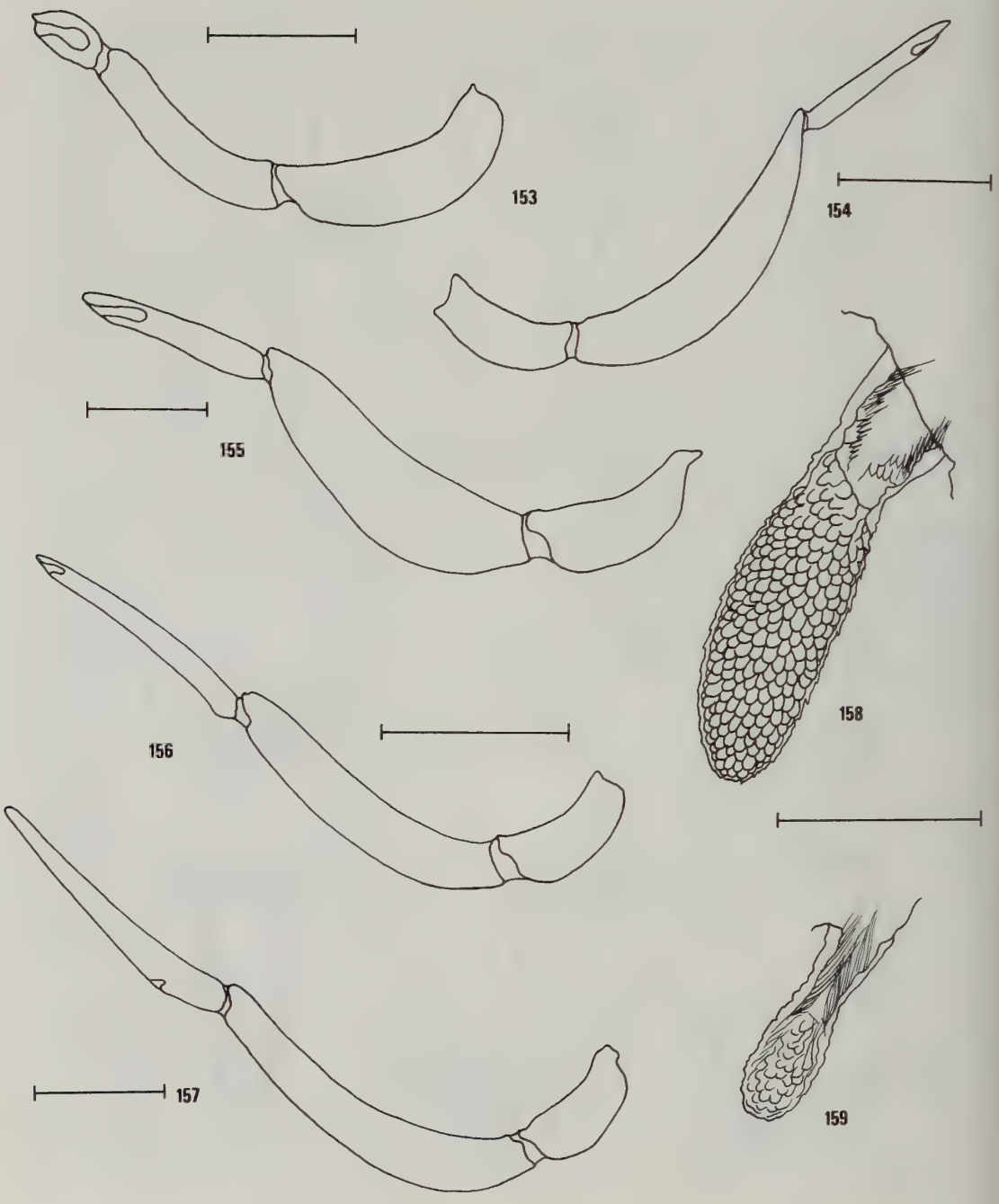
Figs 131–139 131–134, right hindwing venation: (131) *Paectes*; (132) *Autographa gamma*; (133) *Cucullia*; (134) *Lophoptera*. 135, 136, right forewing areoles: (135) *Lophoplusia*; (136) *Lophoptera*. 137–139, right hindwing venation: (137) *Syngrapha (Syngrapha)*; (138) *Chalcopasta*; (139) *Calophasia*, vein M_2 is completely lost in this genus and is represented by a fold depicted as a dashed line.



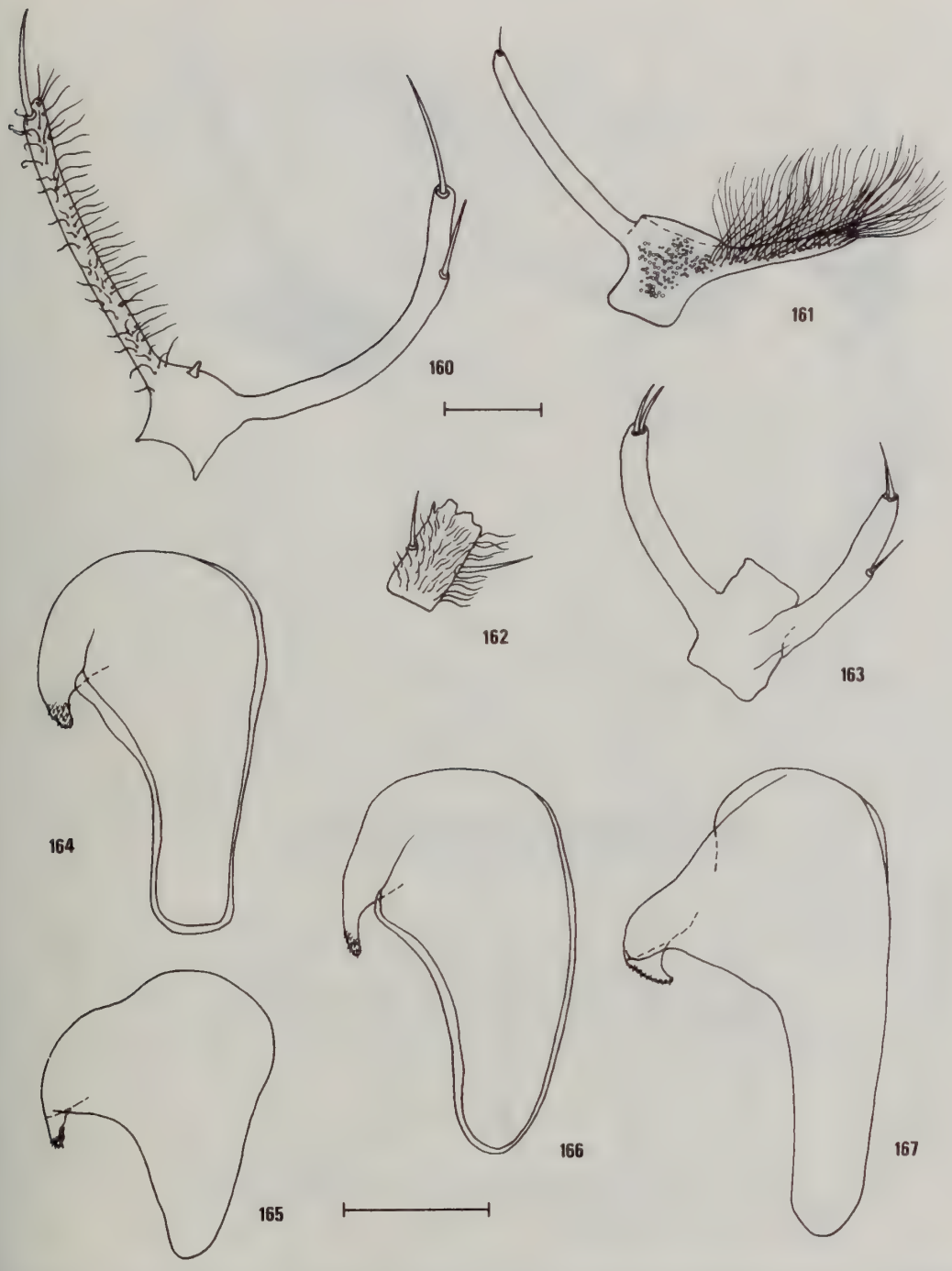
Figs 140–146 140–142, scale base patterns: (140) *Omorphina*; (141) *Sclerogenia*; (142) *Paectes*. 143, tornal angle of *Diloba*, illustrating the apical remnant of vein *CuP*. 144–146, right pilifers, frontal view: (144) *Stictoptera*; (145) *'Autographa' bractea*; (146) *Diloba*. Scale line for Figs 140–142 = 0·1 mm and for Figs 144–146 = 0·2 mm.



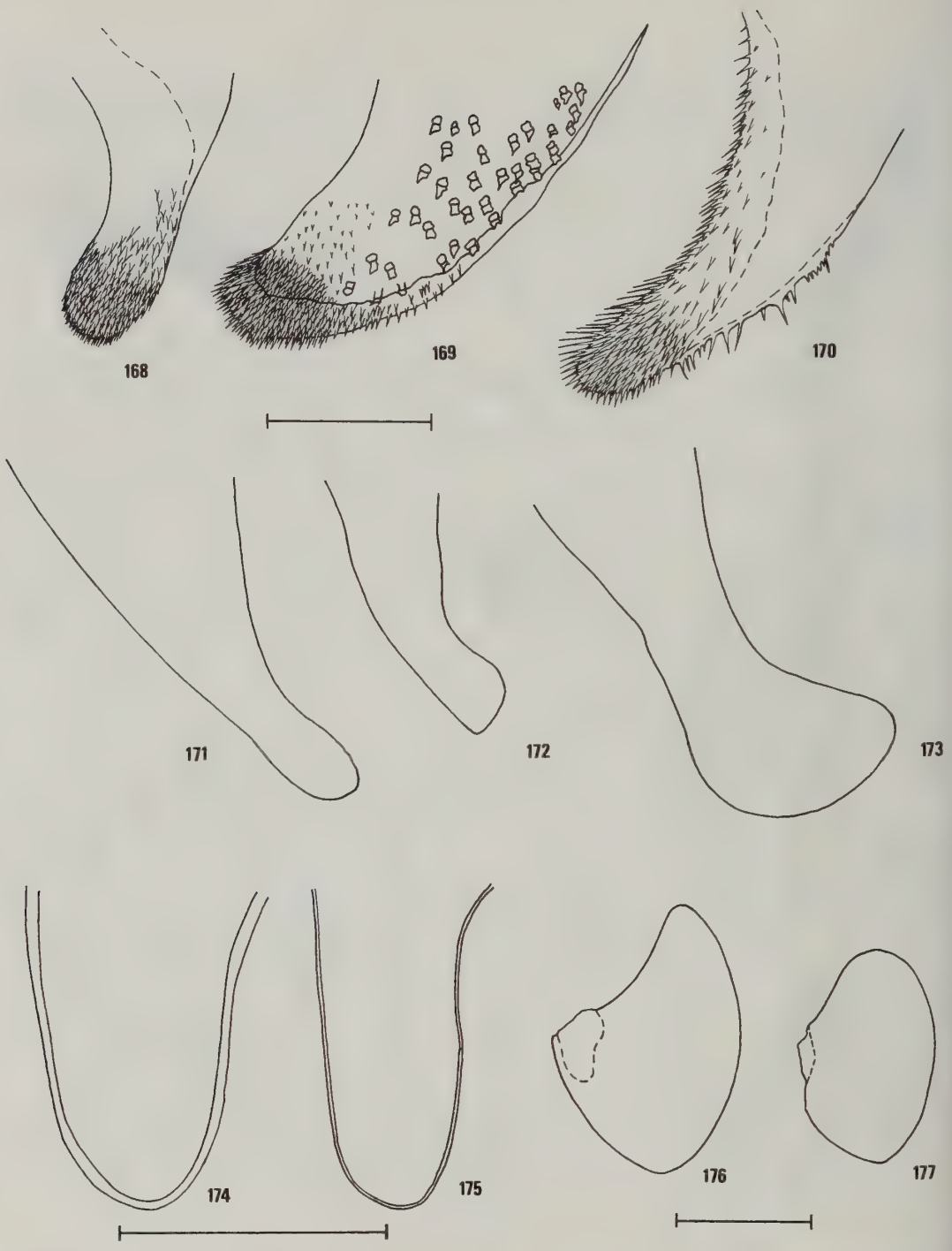
Figs 147–152 Heads. 147, dorsal view, *Mouralia*. 148, lateral view, *Mouralia*. 149, dorsal view, *Anuga*. 150, lateral view, *Anuga*. 151, latero-frontal view, *Syngrapha (Syngrapha)*. 152, frontal view, *Stictoptera*.



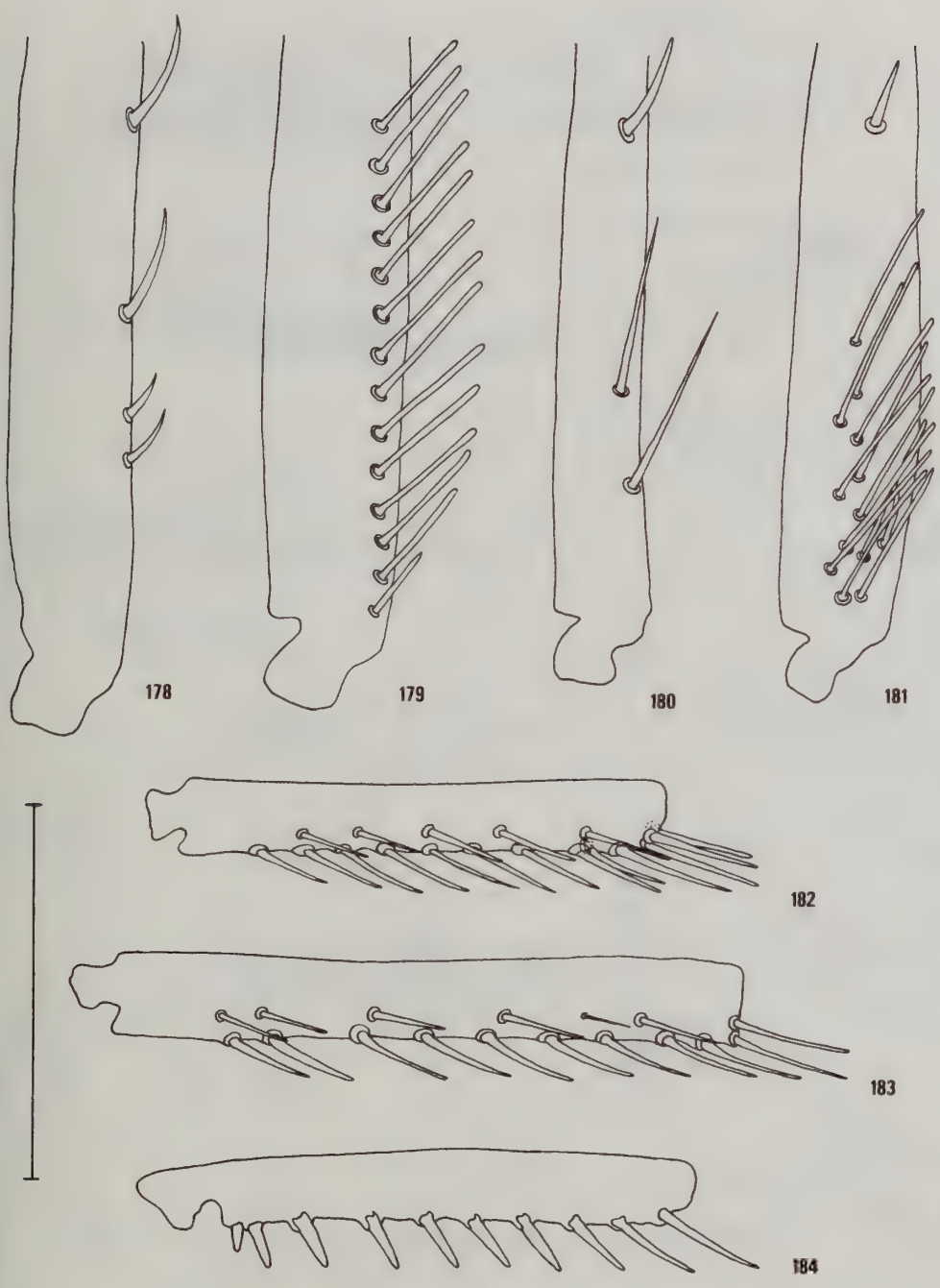
Figs 153–159 153–157, labial palps: (153) *Oncocnemis*; (154) *Panchrysia*; (155) *Anagrapha*; (156) *Chrysanympha*; (157) *Plusiopalpa*. 158, 159, vom Rath's organ tubes: (158) *Stictoptera*; (159) *Abrostola*. Scale lines for Figs 153 and 155 = 0·5 mm and for Figs 158–159 = 0·1 mm.



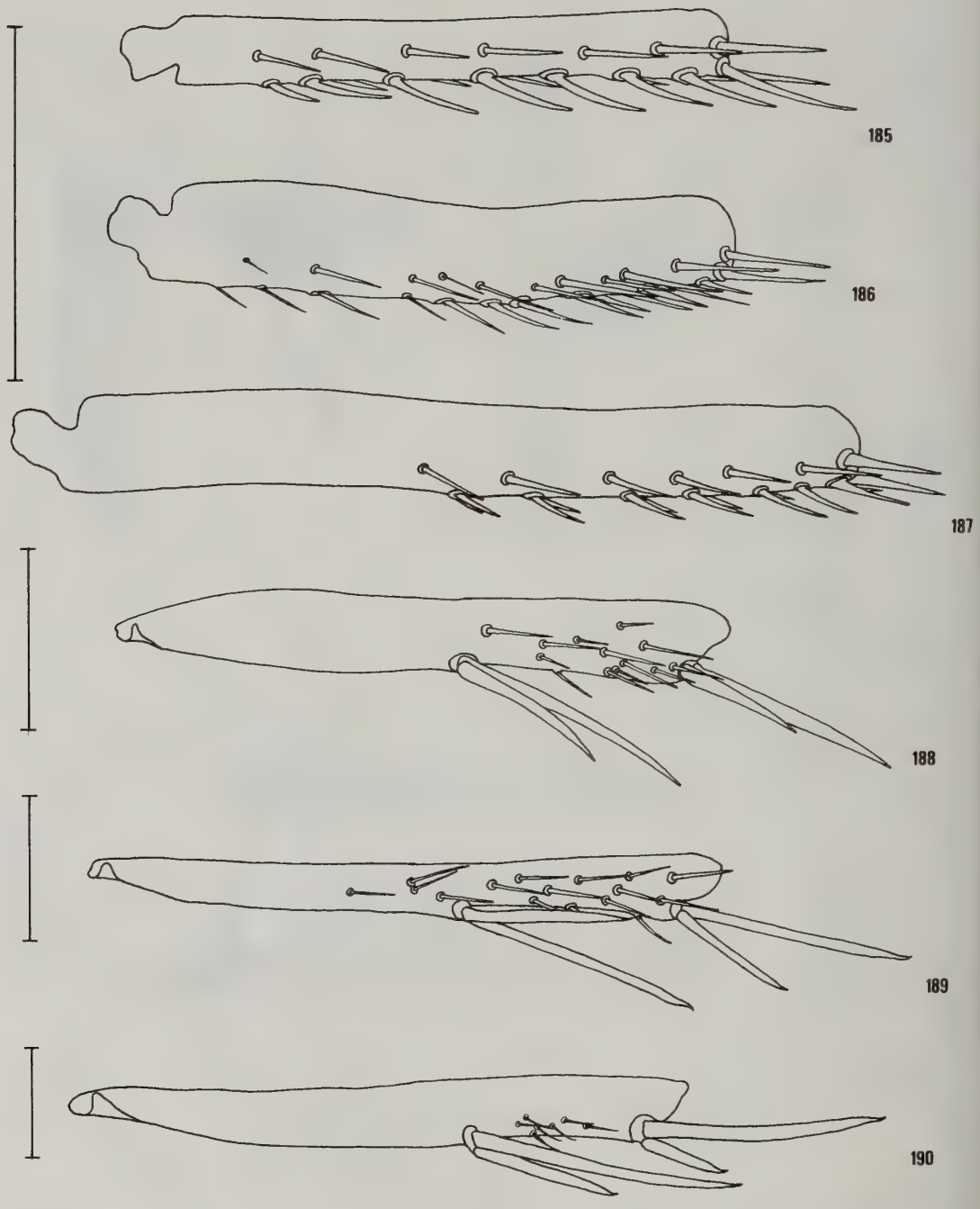
Figs 160–167 160–163, antennal segments: (160) *Lophoplusia*; (161) *Paectes*; (162) *Eosphoropteryx*; (163) *Brachionycha*. 164–167, left tegulae, dorsal view: (164) *Abrostola*; (165) *Diloba*; (166) *Diachrysia*; (167) *Brachionycha*. The broad dorsal arm rests latero-dorsally on the mesothorax while the apically microspinose ventral arm curves underneath the wings.



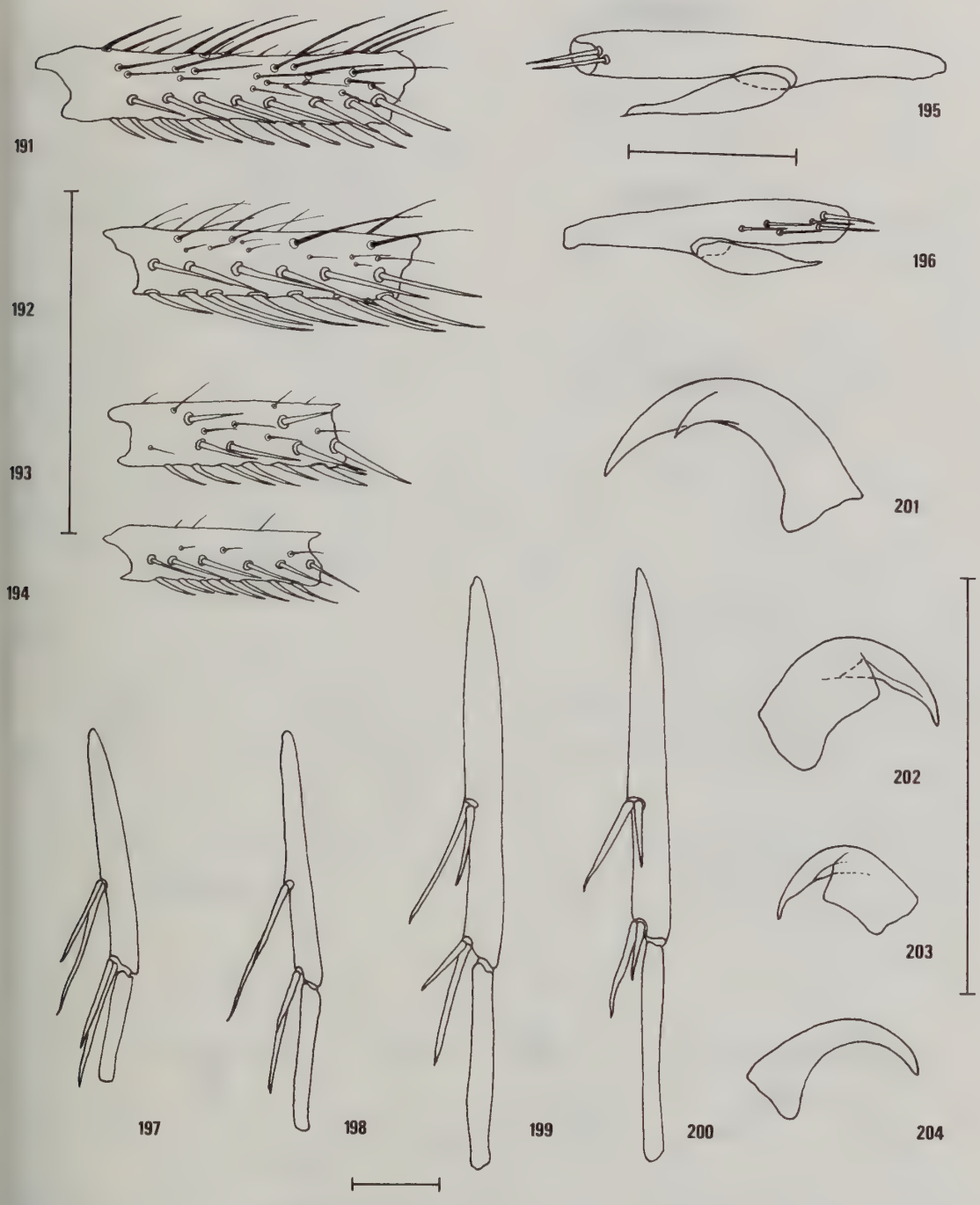
Figs 168–177 168–170, ventral tegular arms, showing microspination: (168) *Plusia*; (169) *Stictoptera*; (170) *Cucullia*. 171–173, outlines of ventral tegular arms: (171) *Syngrapha (Palaeographa)*; (172) *Omorphina*; (173) *Paectes*. 174, 175, outlines of dorsal tegular arms illustrating the marginal flange: (174) *Agrapha*; (175) *Cucullia*. 176, 177, patagia: (176) *Anuga*; (177) *'Autographa' bractea*. The attachment point (dashed outline) is ventral and medial, with the narrower angle (uppermost in these drawings) directed laterally. Scale line for Figs 168–170 = 0·2 mm.



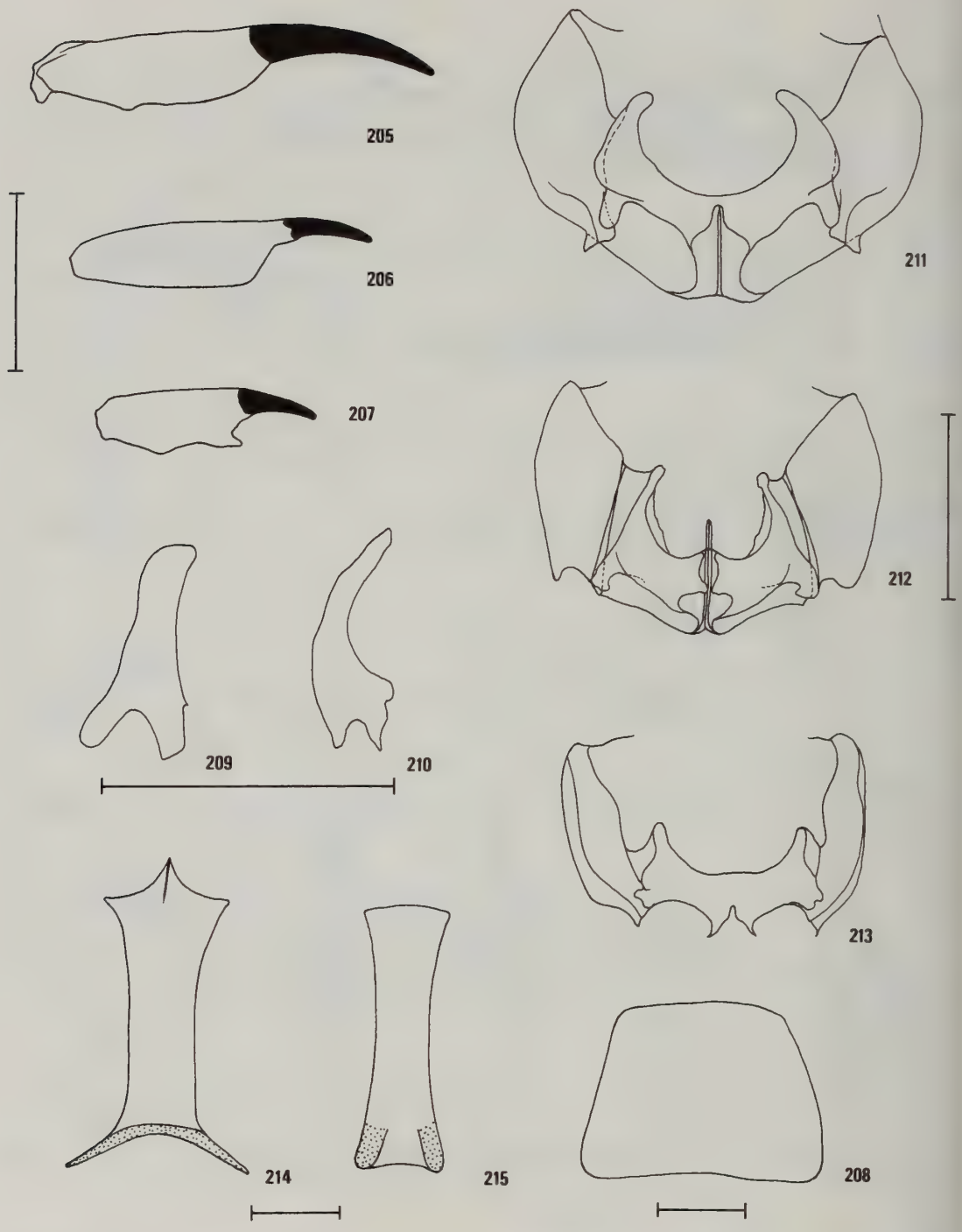
Figs 178–184 178–181, male hind-basitarsi illustrating the basitarsal combs: (178) *Plusiopalpa*; (179) *Thysanoplusia*; (180) *Ctenoplusia (Ctenoplusia)*; (181) *Argyrogramma*. 182–184, male fore-basitarsi: (182) *Plusiotricha (Plusiotricha)*; (183) *Stigmoplusia*; (184) *Argyrogramma*.



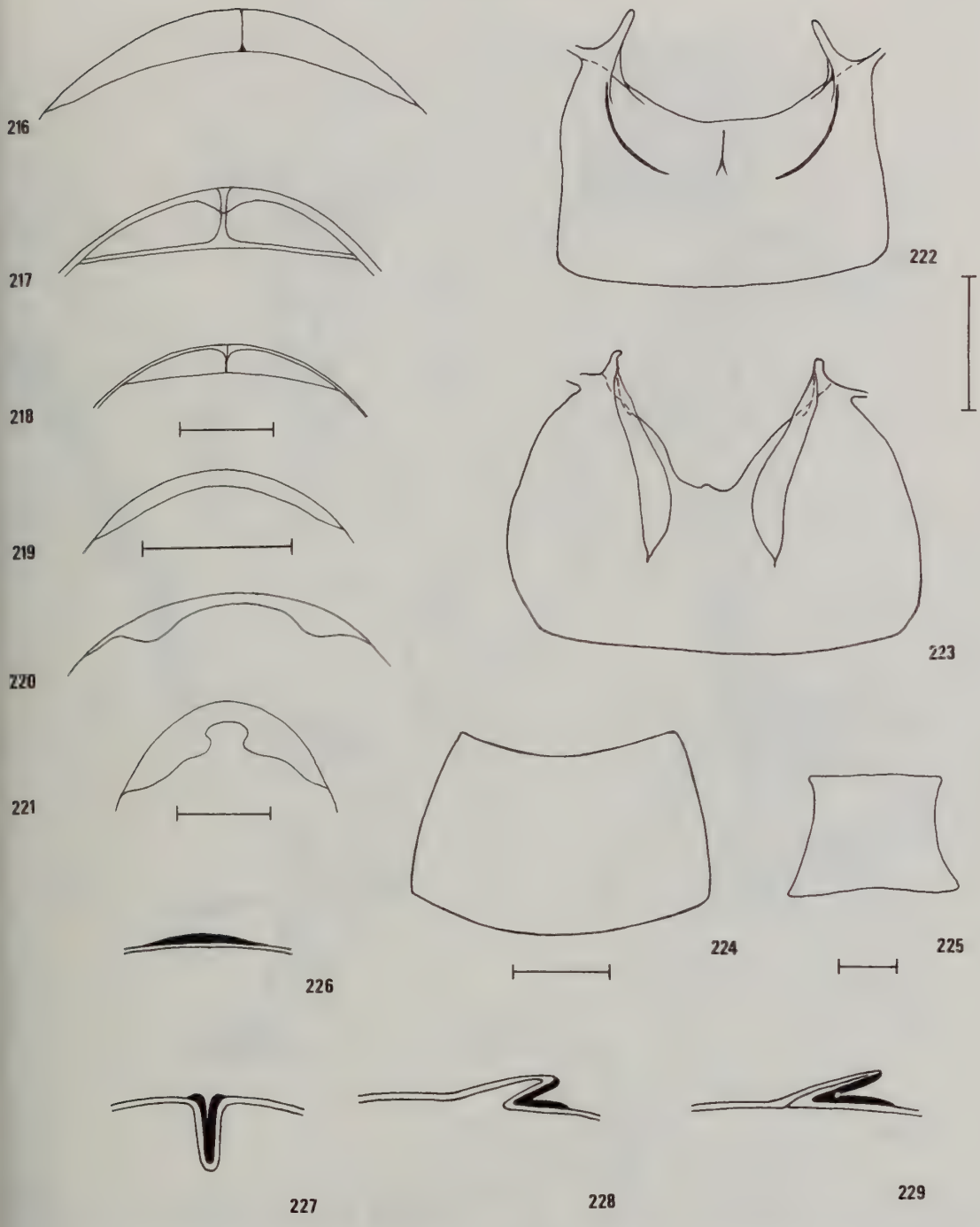
Figs 185–190 185–187, hind-basitarsi: (185) *Anagrapha*; (186) *Paectes*; (187) *Stictoptera*. 188–190, hind-tibiae: (188) outer view, *Syngrapha (Syngrapha)*; (189) outer view, *Rachiplusia*; (190) inner view, *Mouralia*.



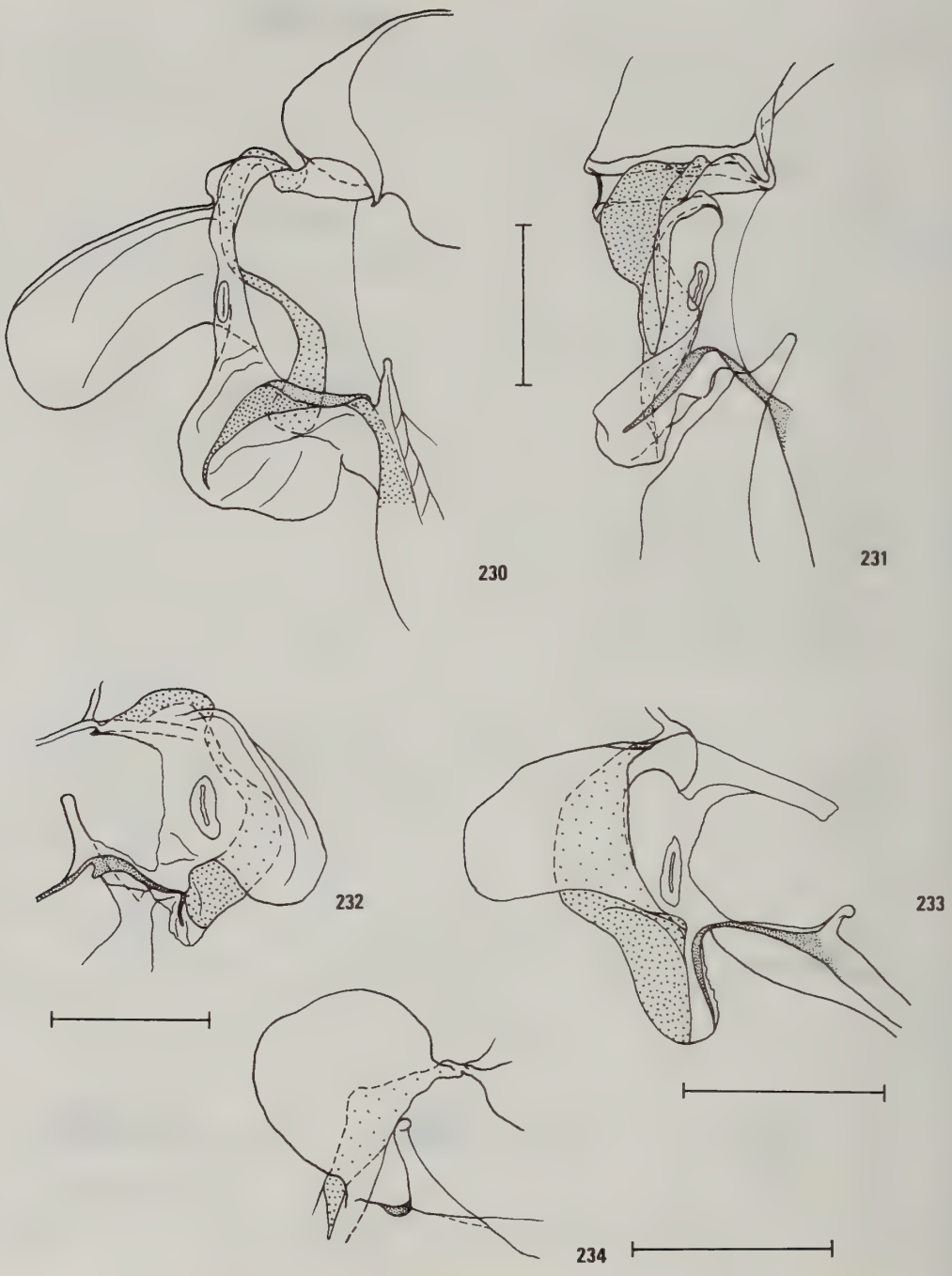
Figs 191–204 191–194, fore-tarsi, third segment: (191) *Lophoplusia*; (192) *Polychrysia*; (193) *Diachrysia*; (194) *Anagrapha*. 195, 196, fore-tibiae: (195) *Rachiplusia*; (196) *Syngrapha (Caloplusia)*. 197–200, outlines of hind-tibiae, tibial spurs and basitarsi: (197) *Anuga*; (198) *Stictoptera*; (199) *'Autographa' bractea*; (200) *Euchalcia (Euchalcia)*. 201–204, tarsal claws: (201) *Cucullia*; (202) *Autographa gamma*; (203) *Plusiopalpa*; (204) *Oncocnemis*. Scale line for Figs 201–204 = 0·5 mm.



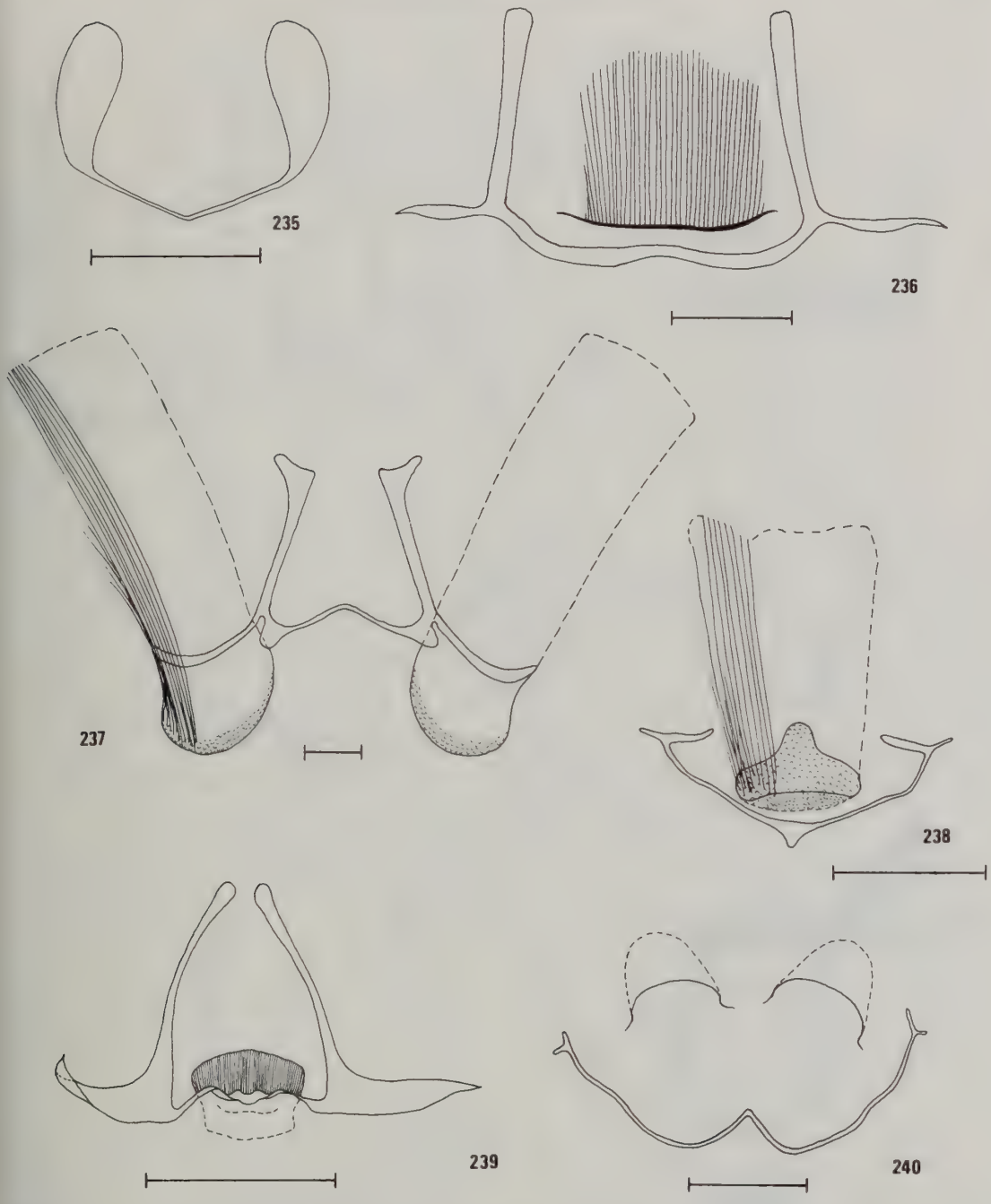
Figs 205–215 205–207, clawed fore-tibiae: (205) *Brachionycha*; (206) *Chalcopasta*; (207) *Oncocnemis*. 208, male St7, anterior edge uppermost, *Anadevidia*. 209, 210, lateral views from left of prothoracic furcae: (209) *Lophoplusia*; (210) *Anuga*. 211–213, prothoracic furcae and epimera, posterior views: (211) *Lophoplusia*; (212) *Paectes*; (213) *Diloba*. 214, 215, male St7s, anterior edges uppermost: (214) *Stigmoplusia*; (215) *Argyrogramma*.



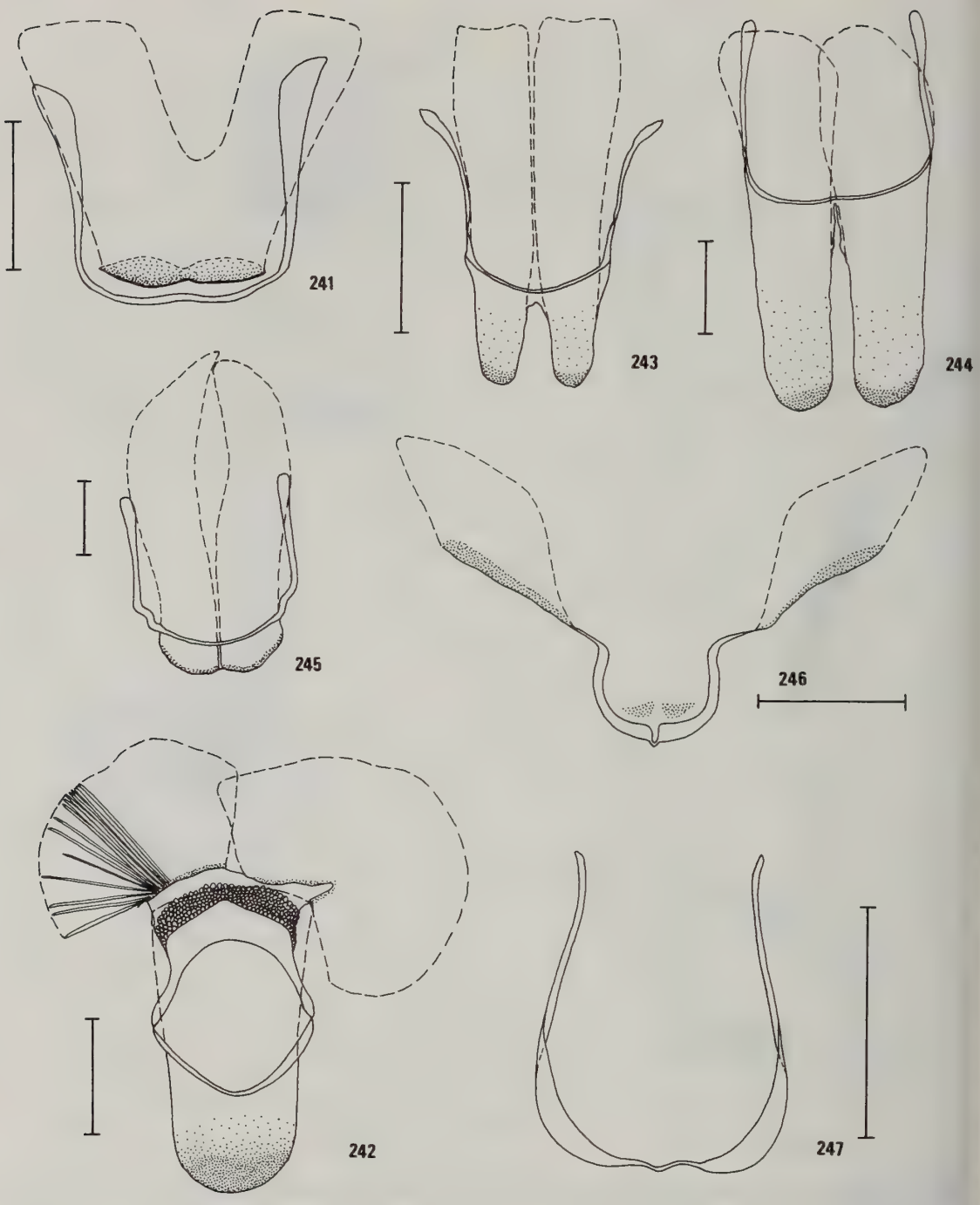
Figs 216–229 216–221, internal flanges on the anterior edges of T2: (216) *Cucullia*; (217) *Stictoptera*; (218) *Lophoptera*; (219) *Omorphina*; (220) *Abrostola*; (221) *Anagrapha*. 222, 223, St2's, anterior edges uppermost: (222) *Syngrapha (Caloplusia)*; (223) *Paectes psaliphora* Hampson. 224, 225, female T7's, posterior edges uppermost: (224) *Adeva*; (225) *Autoplusia egena*. 226–229, diagrammatic cross-sections of dorso-lateral scent patches on male T7's; scale arbitrary: (226) *Agrapha*; (227) *Dactyloplusia*; (228) *Ctenoplusia (Ctenoplusia)*; (229) *Argyrogramma*.



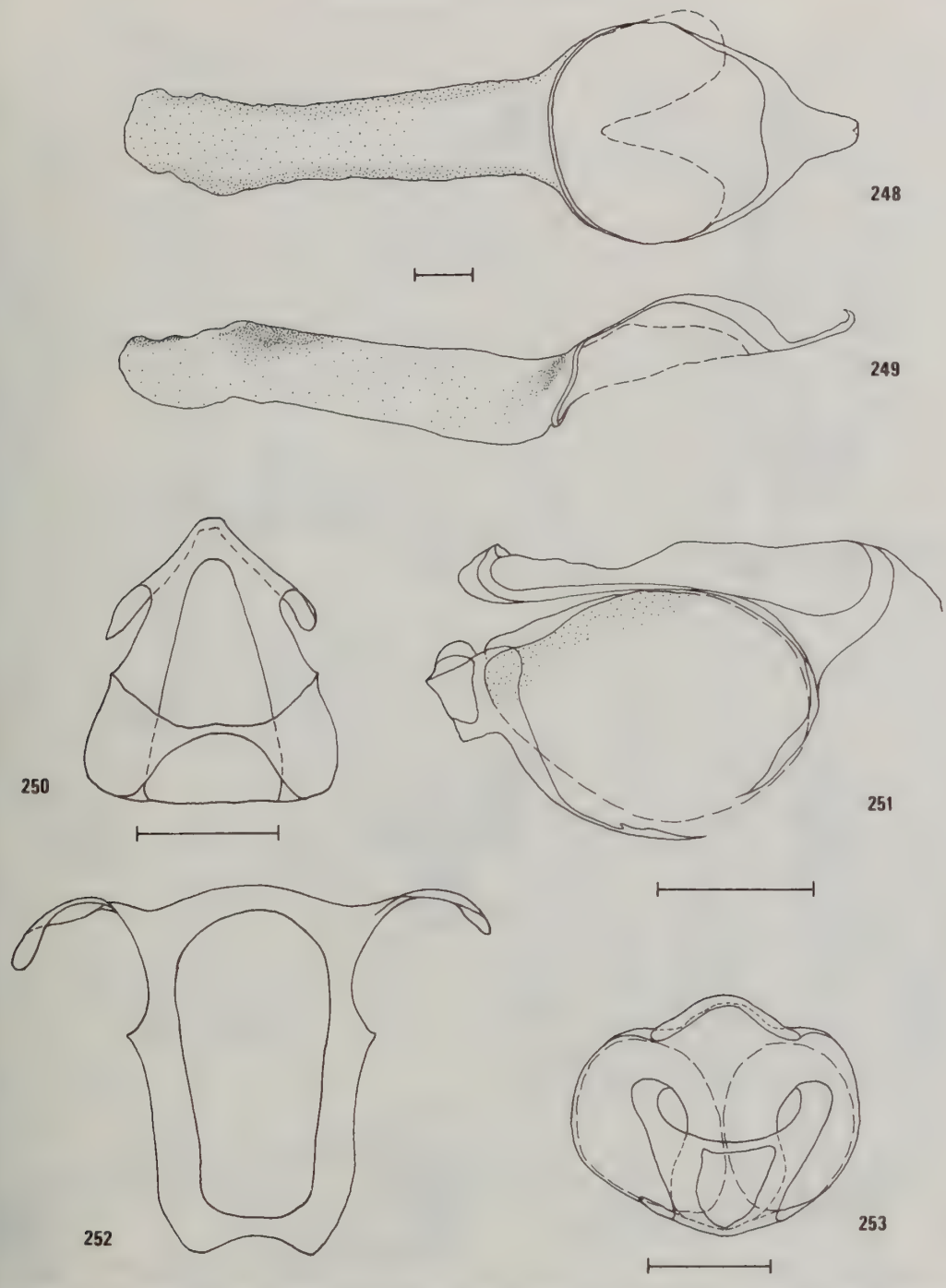
Figs 230–234 Counter tympanal hoods and pleural pouches. The apodemes from St2 and the post-spiracular bars are shaded. 230, anterior view, RHS, *Thysanoplusia orichalcea*. 231, lateral view, RHS, *Thysanoplusia orichalcea*. 232, anterior view, LHS, *Panchrysia*. 233, anterior view, RHS, *Stictoptera*. 234, anterior view, RHS, *Calophasia*.



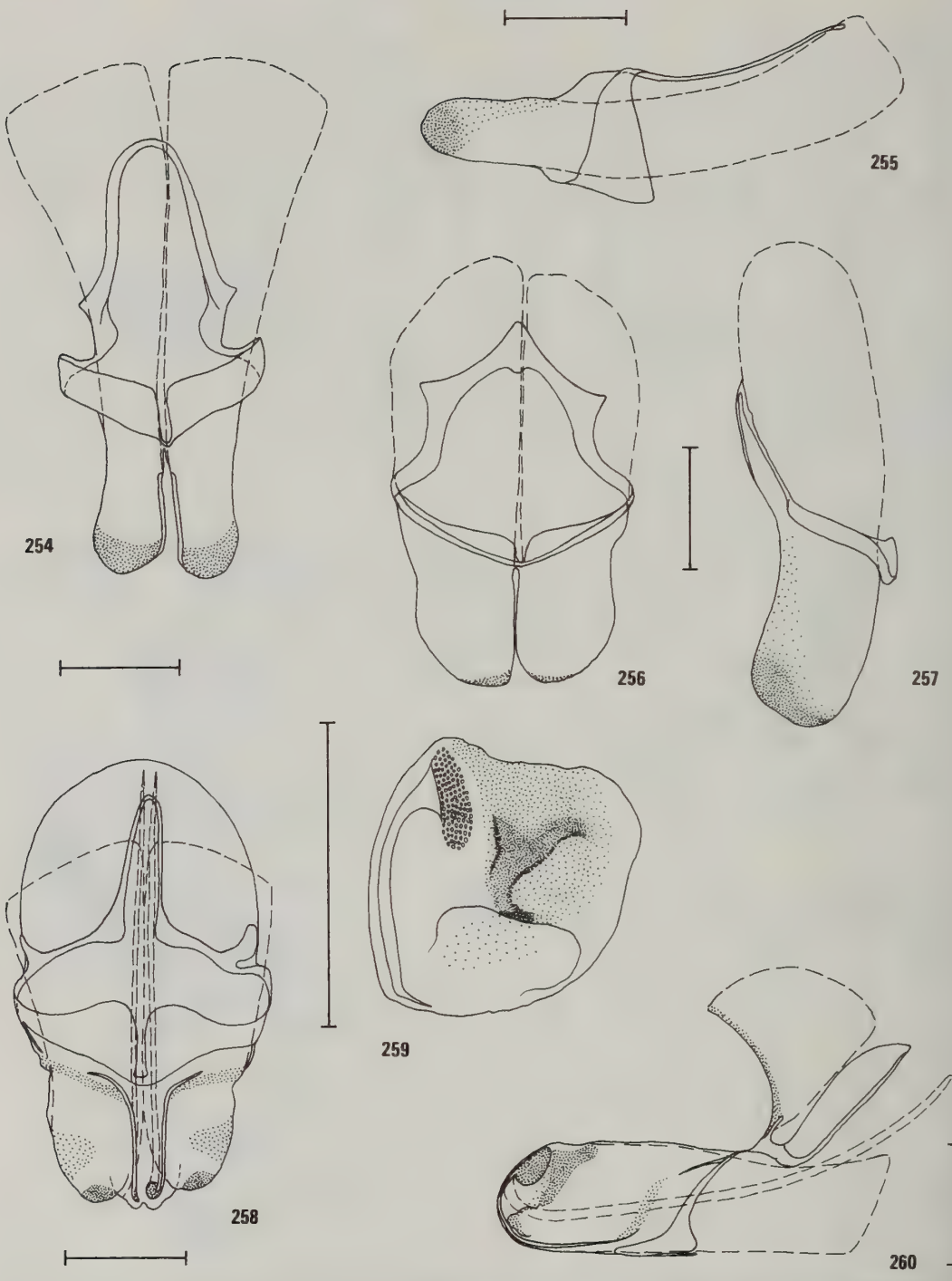
Figs 235–240 St8 and sternal hair pencils, ventral views. 235, *Brachionycha*, hair pencils absent. 236, *Cucullia*, hair pencil represented by a sparse tuft of scales arising from a sclerotized line. 237, *Magusa*, the lateral arms of St8 have been flattened so that the hair pencils have been turned outwards through 90°. 238, *Paectes*. 239, *Stictoptera*. 240, *Anuga*, the hair pencil pockets have been turned through 180° so as to face anteriorly instead of posteriorly. In Figs 237 and 238, and in subsequent illustrations of hair pencils, the pencils themselves are not drawn in detail but their limits are shown by dashed lines. If limits are not shown, this indicates that the hair pencil scales had become detached before drawing. In addition, the shading at the base of the pockets indicates the extent of the main fields of hair pencil scale insertions.



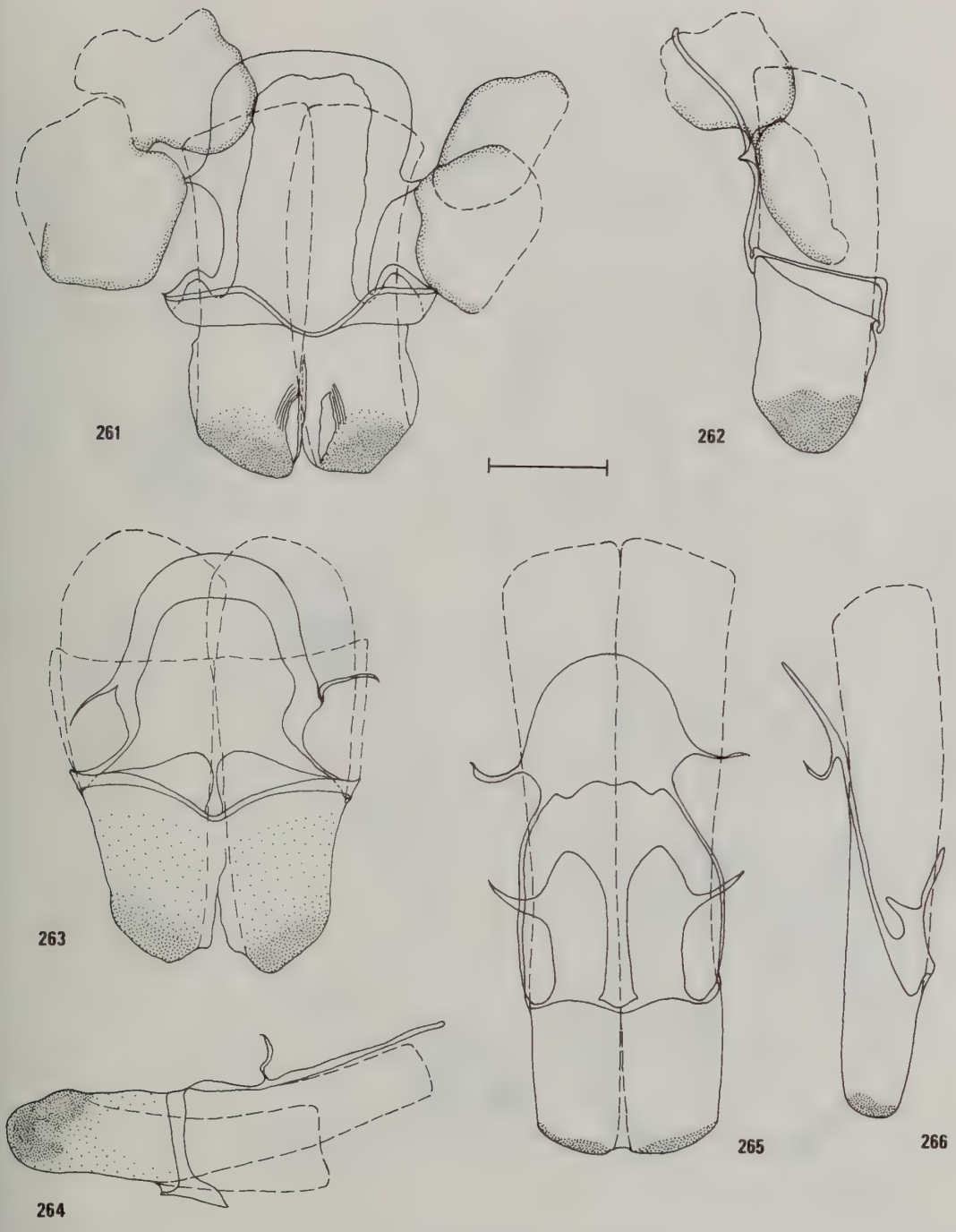
Figs 241–247 St8 and sternal hair pencils, ventral views. 241, *Lamprotes*. 242, *Chrysodeixis (Chrysodeixis) argentifera*. Note the expanded secondary hair brushes, the spatulate apical scales and the complete fusion of the hair pencils and their pockets. 243, *Macdunnoughia (Macdunnoughia)*. 244, *Autoplusia olivacea*. 245, *'Autographa' bractea*. 246, *Plusiotricha (Eutheiaplusia)*. Note the reduced hair pencils and reduced secondary hair brushes. 247, *Chrysodeixis (Pseudoplusia)*. Note the total loss of all hair pencils and brushes.



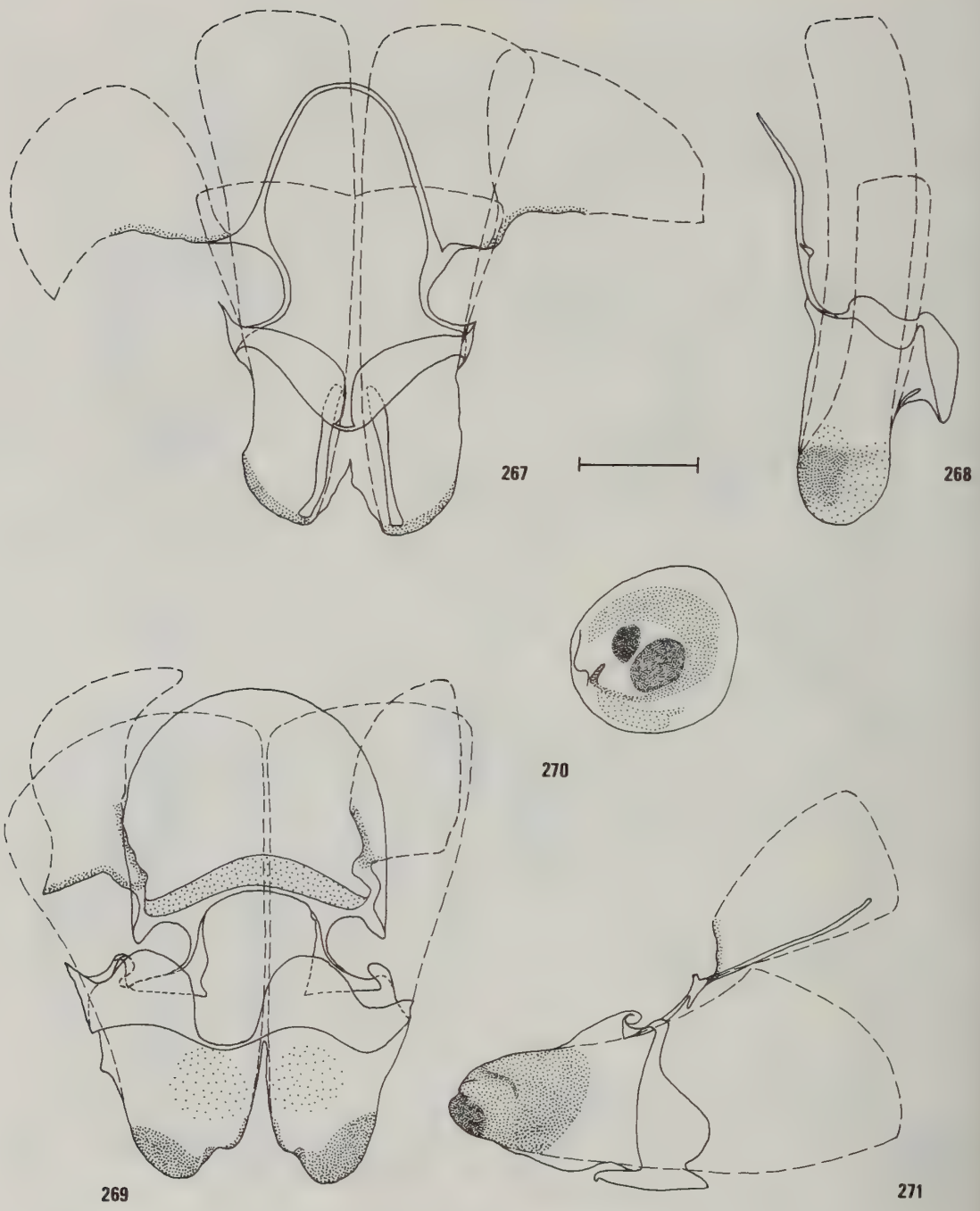
Figs 248–253 248, 249, St8 and hair pencil of *Mouralia*: (248) ventral view; (249) lateral view. 250–253, A8 and hair pencil structures of *Chrysodeixis (Chrysodeixis) chalcites*: (250) St8, posterior edge uppermost; (251) lateral view of A8 and hair pencil complex; note how the sagittate St8 supports the almost spherical hair brush ventrally, while T8 supports it dorsally, with the lateral arms of T8 curving laterally and ventrally to support the mouth of the hair brush pocket; (252) T8, posterior edge uppermost; (253) anterior view of A8 and the hair pencil complex, showing how the anterior part of St8 supports the bases of the hair brushes.



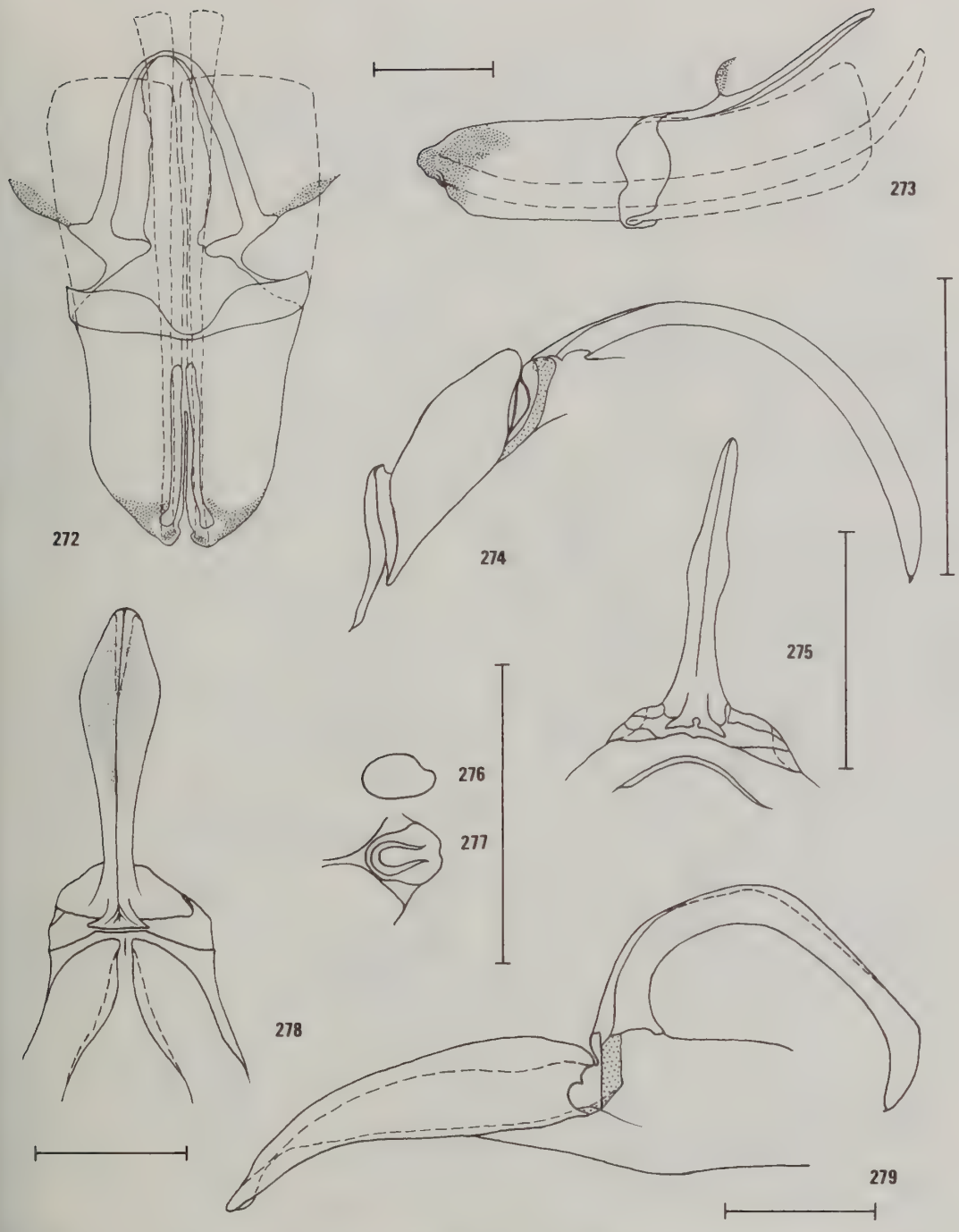
Figs 254–260 St8 and sternal hair pencils. 254, *Trichoplusia*, ventral view. 255, *Trichoplusia*, lateral view. 256, *Thysanoplusia*, ventral view. 257, *Thysanoplusia*, lateral view. 258, *Argyrogramma*, ventral view; note the differentiation of the hair pencil scale insertions and the large semicircular flange of scales attached to the apex of the dorsal arms of St8. 259, *Argyrogramma*, anterior view of left hair pencil pocket, showing the different fields of hair pencil scale insertions, dorsal side is uppermost. 260, *Argyrogramma*, lateral view; note the long, thin, curved scales arising from the spatulate area of scale bases and projecting beyond the main hair pencils.



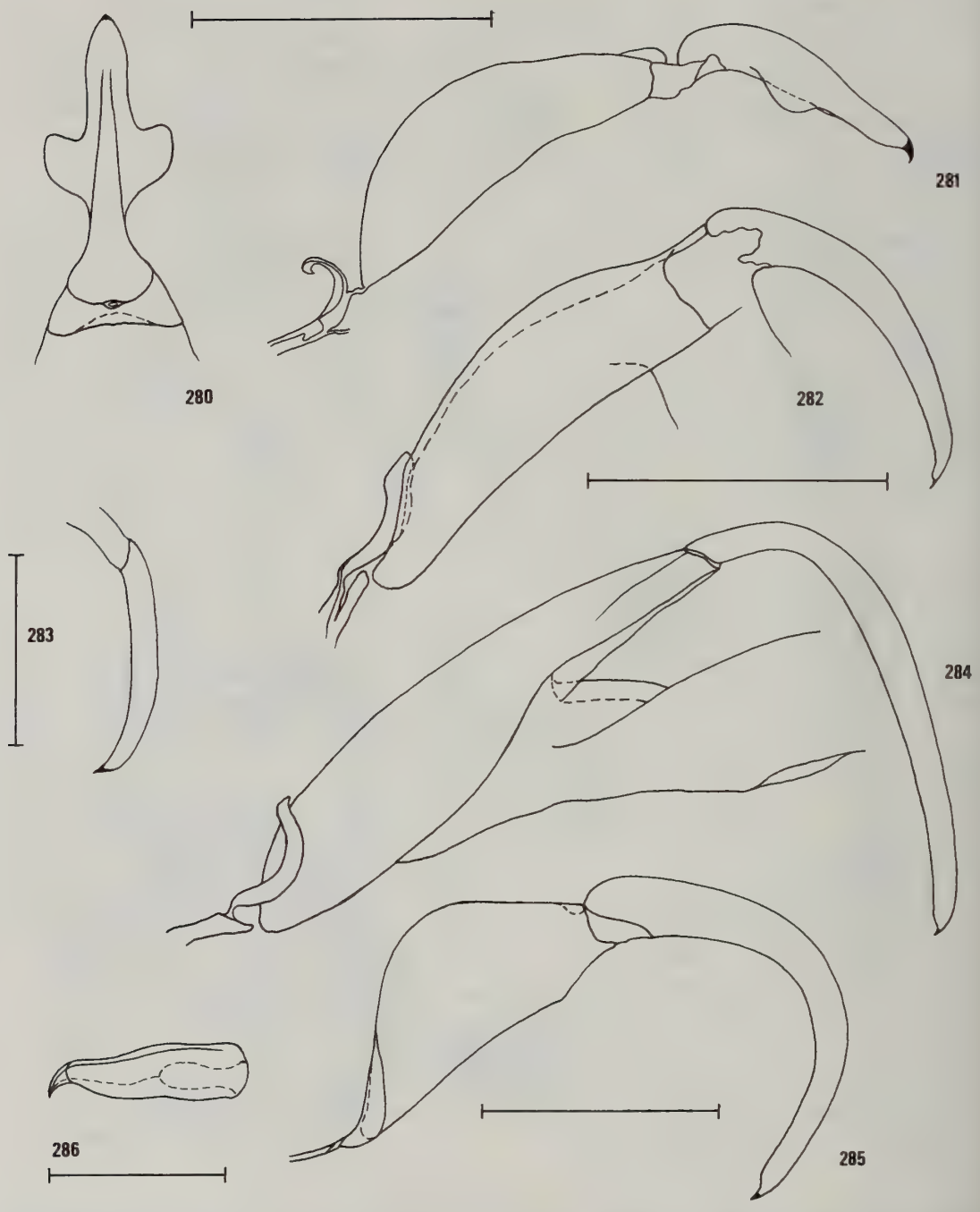
Figs 261–266 St8 and sternal hair pencils. 261, *Plusiotricha (Plusiotricha)*, ventral view. 262, *Plusiotricha (Plusiotricha)*, lateral view; note the large secondary hair brushes. 263, *Ctenoplusia (Acanthoplusia)*, ventral view. 264, *Ctenoplusia (Acanthoplusia)*, lateral view. 265, *Plusiopalpa*, ventral view. 266, *Plusiopalpa*, lateral view.



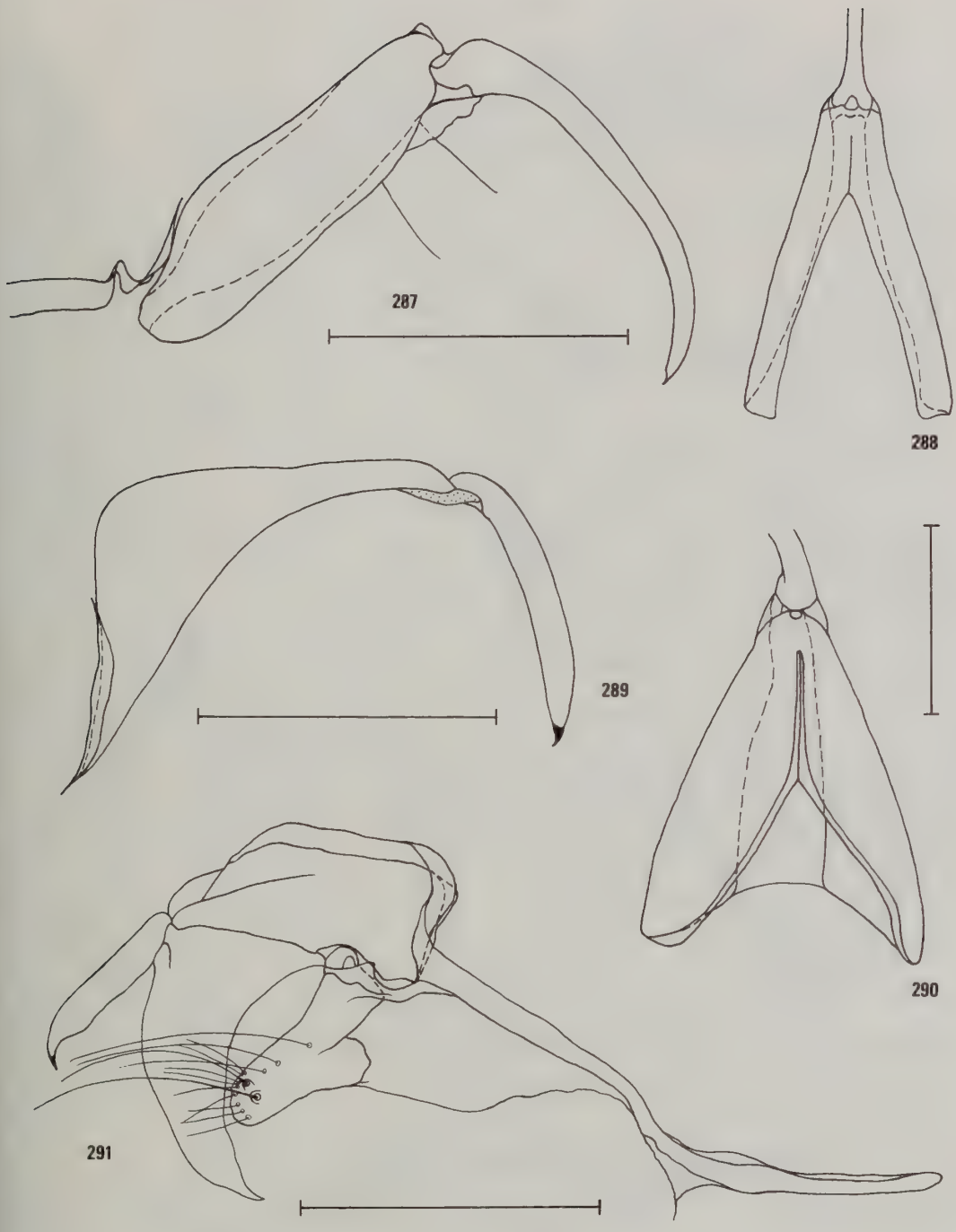
Figs 267–271 St8 and sternal hair pencils. 267, *Ctenoplusia (Ctenoplusia)*, ventral view. 268, *Ctenoplusia (Ctenoplusia)*, lateral view; note that the outer hair pencil scales are shorter than the inner scales. 269, *Stigmoplusia*, ventral view; note the large semicircular flange of scales attached to the dorsal arms of St8. 270, *Stigmoplusia*, anterior view of left hair pencil pocket; note the differentiated fields of hair pencil scale bases. 271, *Stigmoplusia*, lateral view.



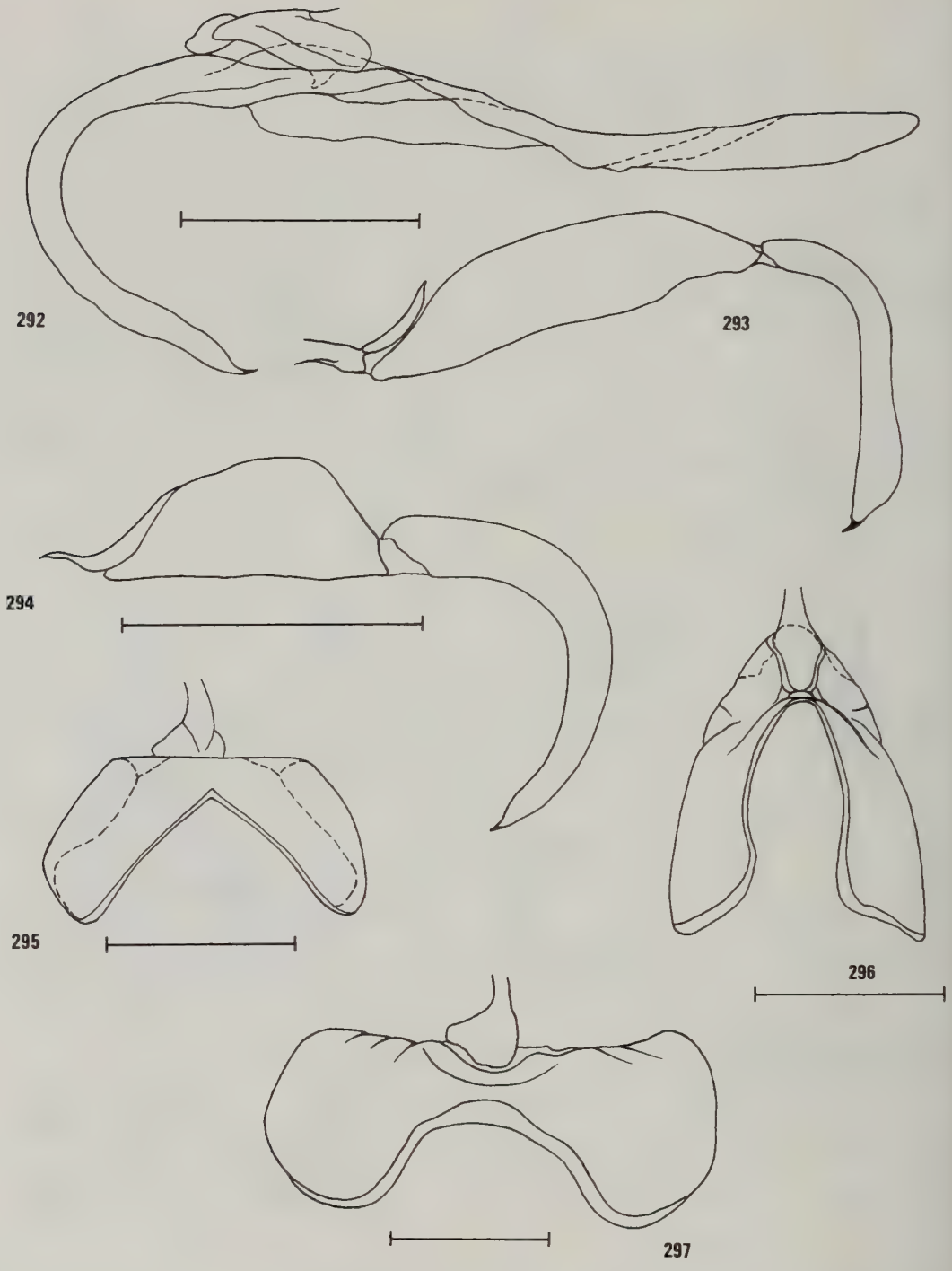
Figs 272–278 272, 273, St8 and sternal hair pencils, *Agrapha*: (272) ventral view; (273) lateral view; note the differentiated hair pencils, similar to the condition seen in *Argyrogramma* (Figs 258–260). 274–279, unci: (274) *Abrostola*, lateral view; (275) *Abrostola*, dorsal view; (276) *Anuga*, lateral view; (277) *Anuga*, lateral view; (278) *Mouralia*, dorsal view; (279) *Mouralia*, lateral view. In Figs 274 and 279, the LAST's are shaded, while the shading on Fig. 278 indicates the field of long, deciduous hairs that arise on the uncus of this genus.



Figs 280–286 Unci and tegumena. 280, *Stigmoplusia*, dorsal view. Note the lateral flanges that are unique to certain members of this genus. 281, *Stigmoplusia*, lateral view. 282, *Oncocnemis*, lateral view. 283, *Syngrapha (Caloplusia)*, lateral view. 284, *Trichoplusia*, lateral view. 285, *Euchalcia (Euchalcia)*, lateral view. 286, *Anuga*, dorso-lateral view. Scale line for Fig. 286 = 0·5 mm.



Figs 287–291 287–290, unci and tegumena: (287) *Macdunnoughia (Macdunnoughia)*, lateral view; (288) *Anadevidia*, dorsal view; (289) *Chrysodeixis (Chrysodeixis)*, lateral view; the LAST has been shaded; (290) *Anagrapha*, dorsal view. 291, lateral view of the terminal segments of *Paectes*, to illustrate the setose socii and the beak-like gnathos. The valves have been removed.



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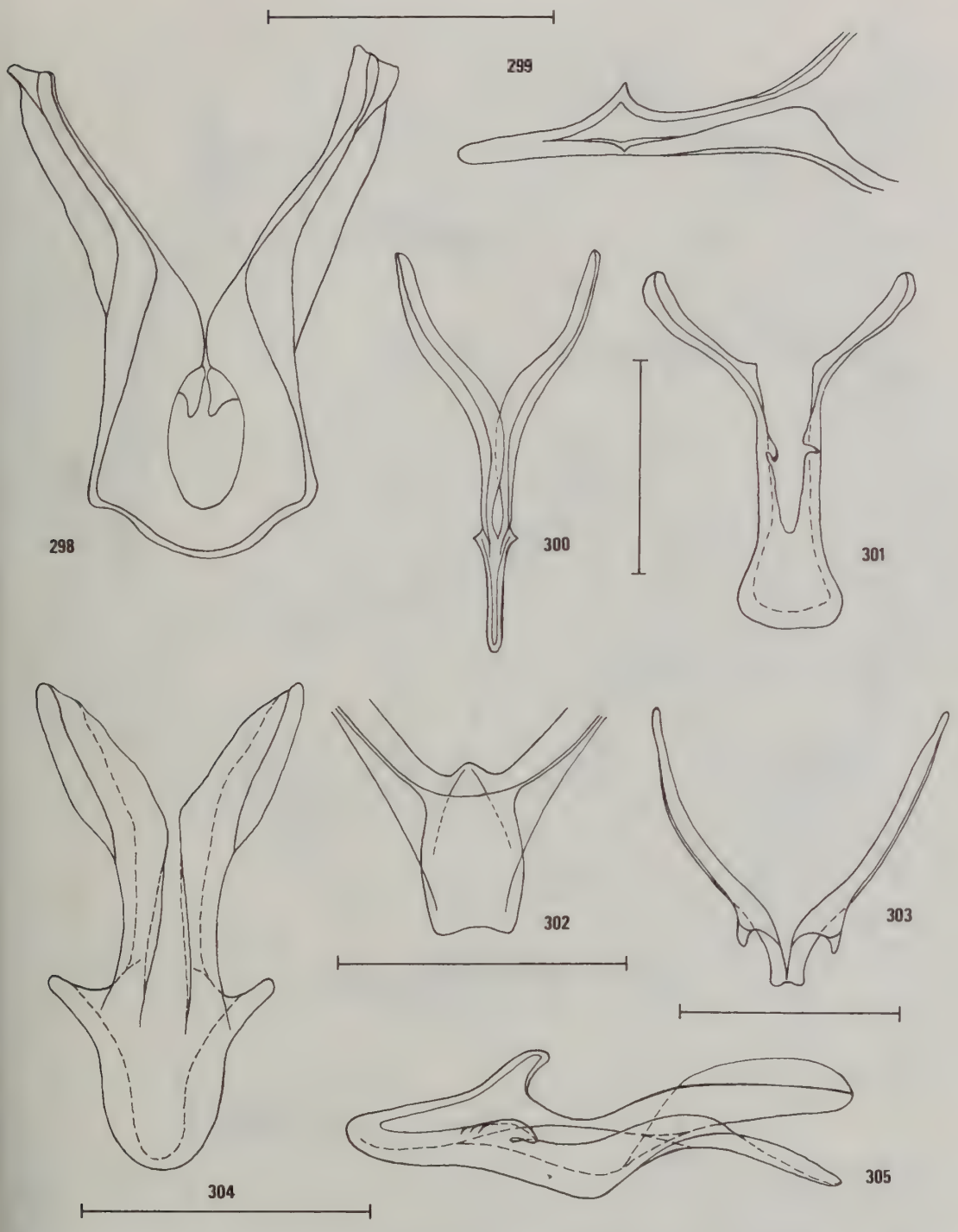

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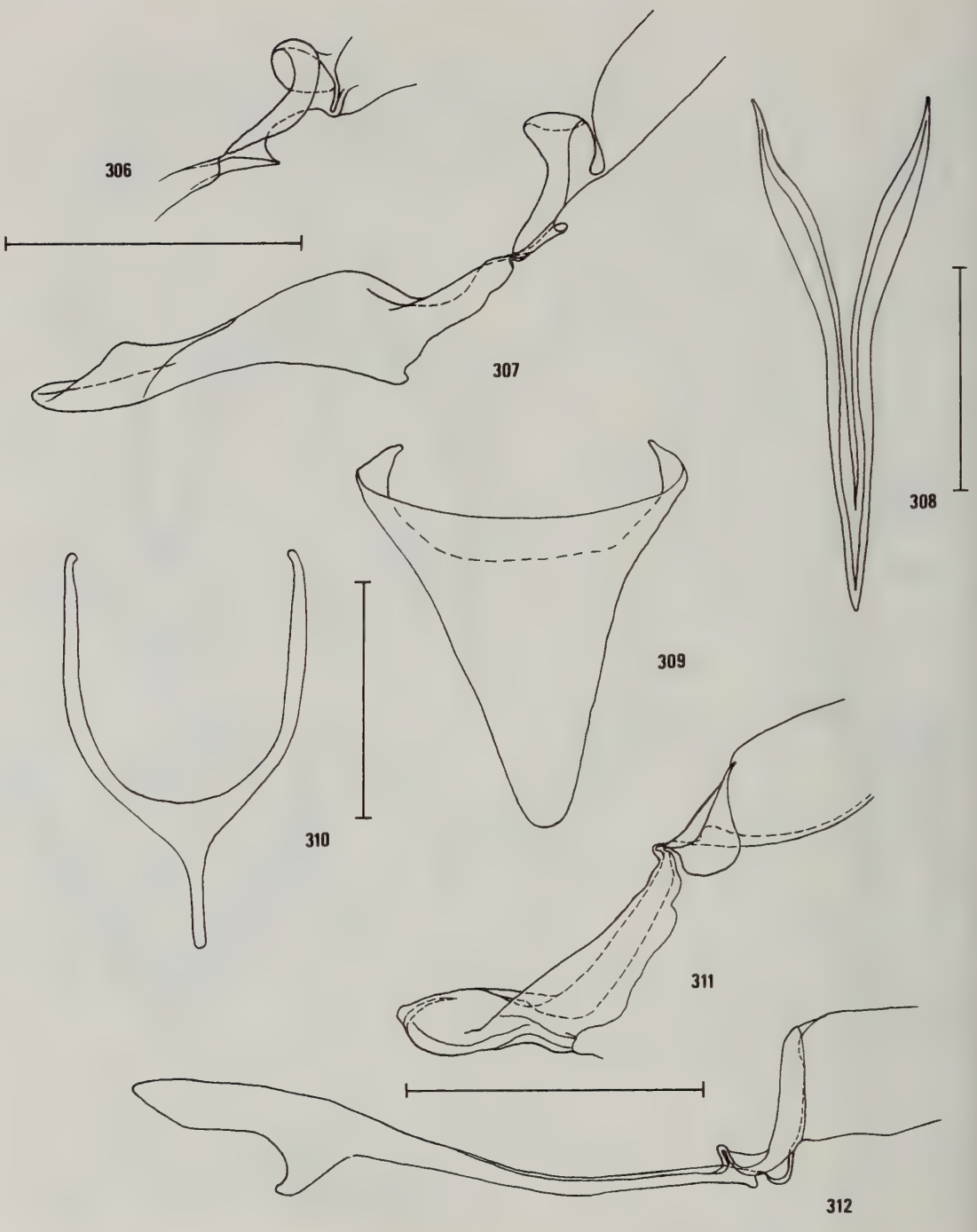

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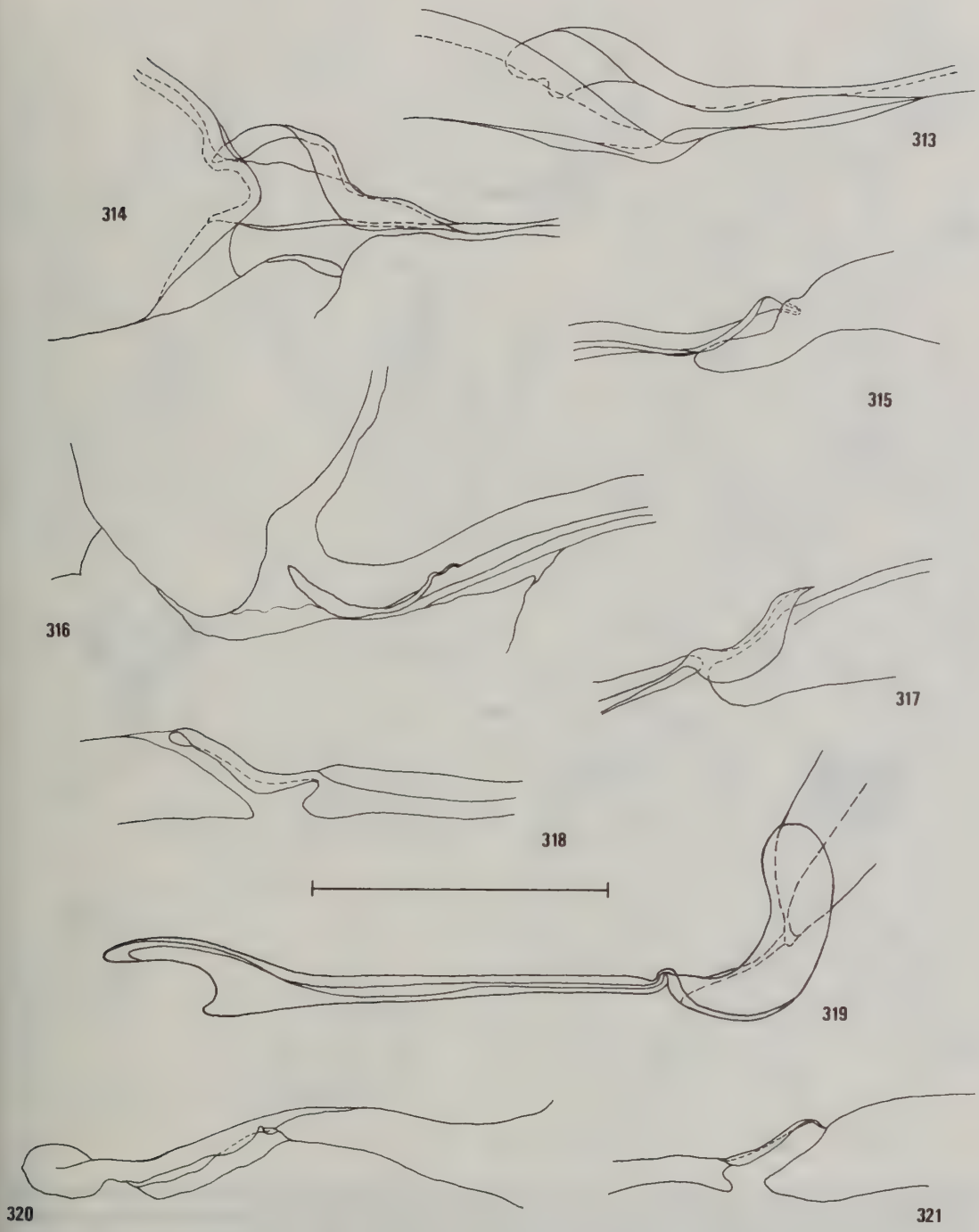

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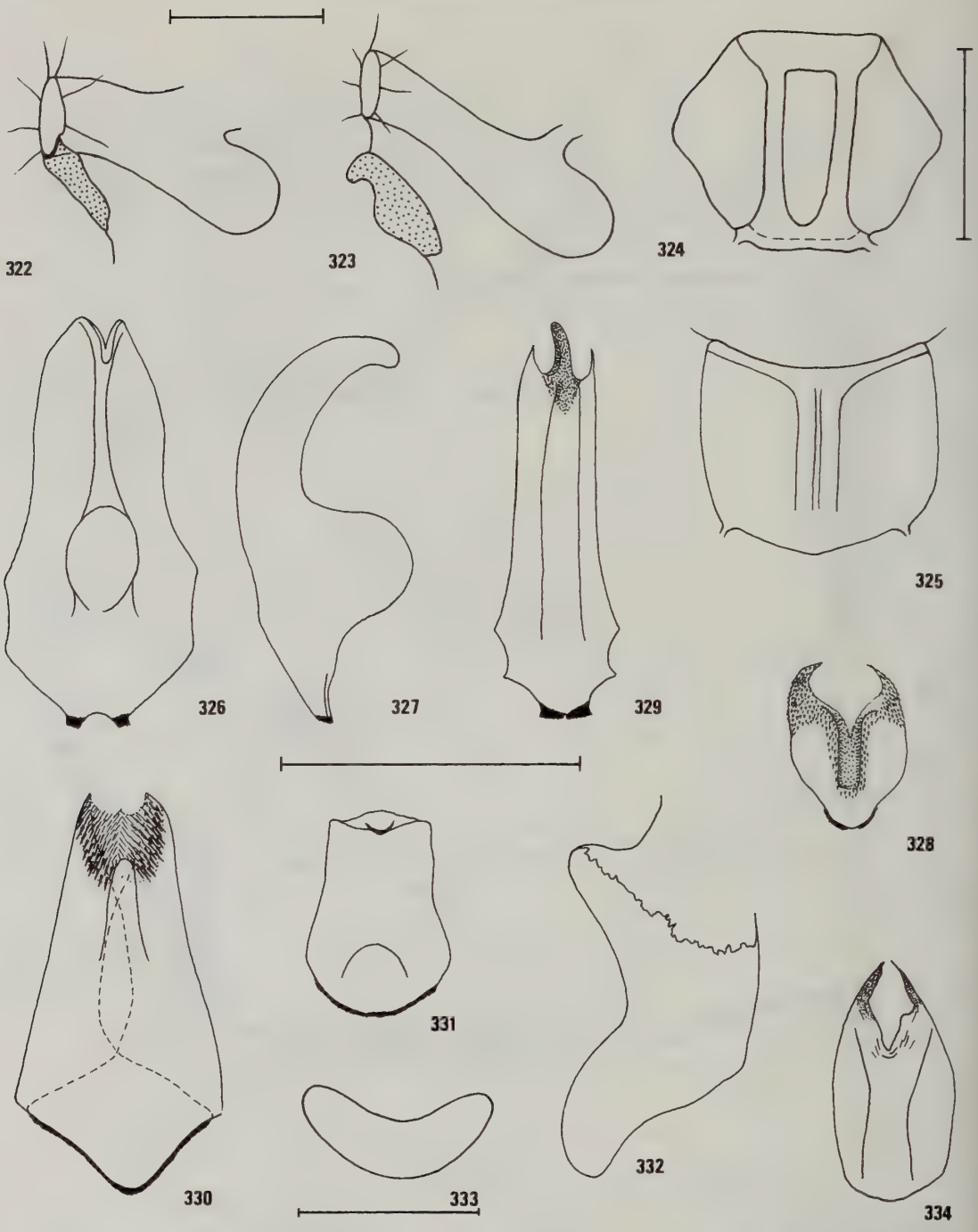

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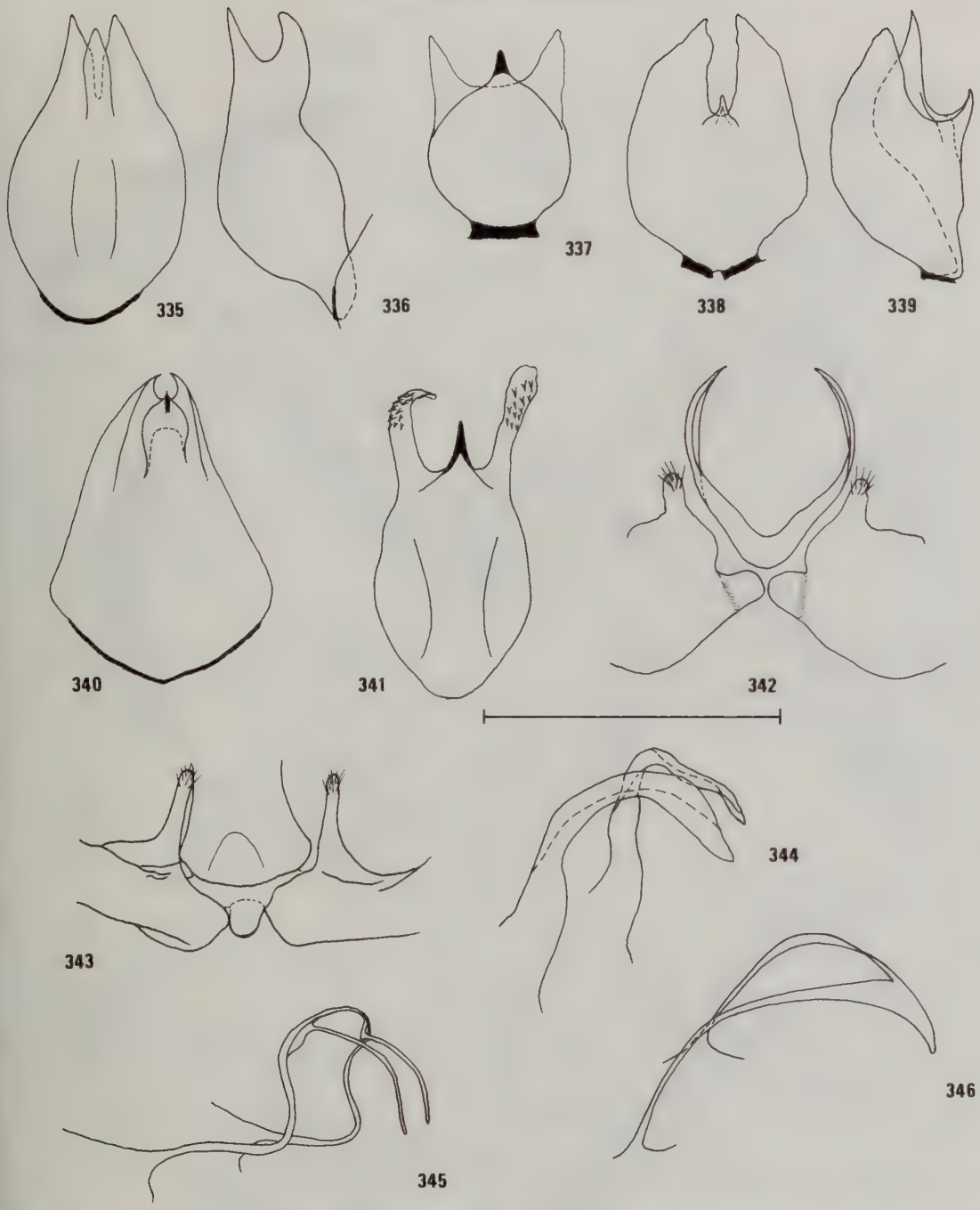

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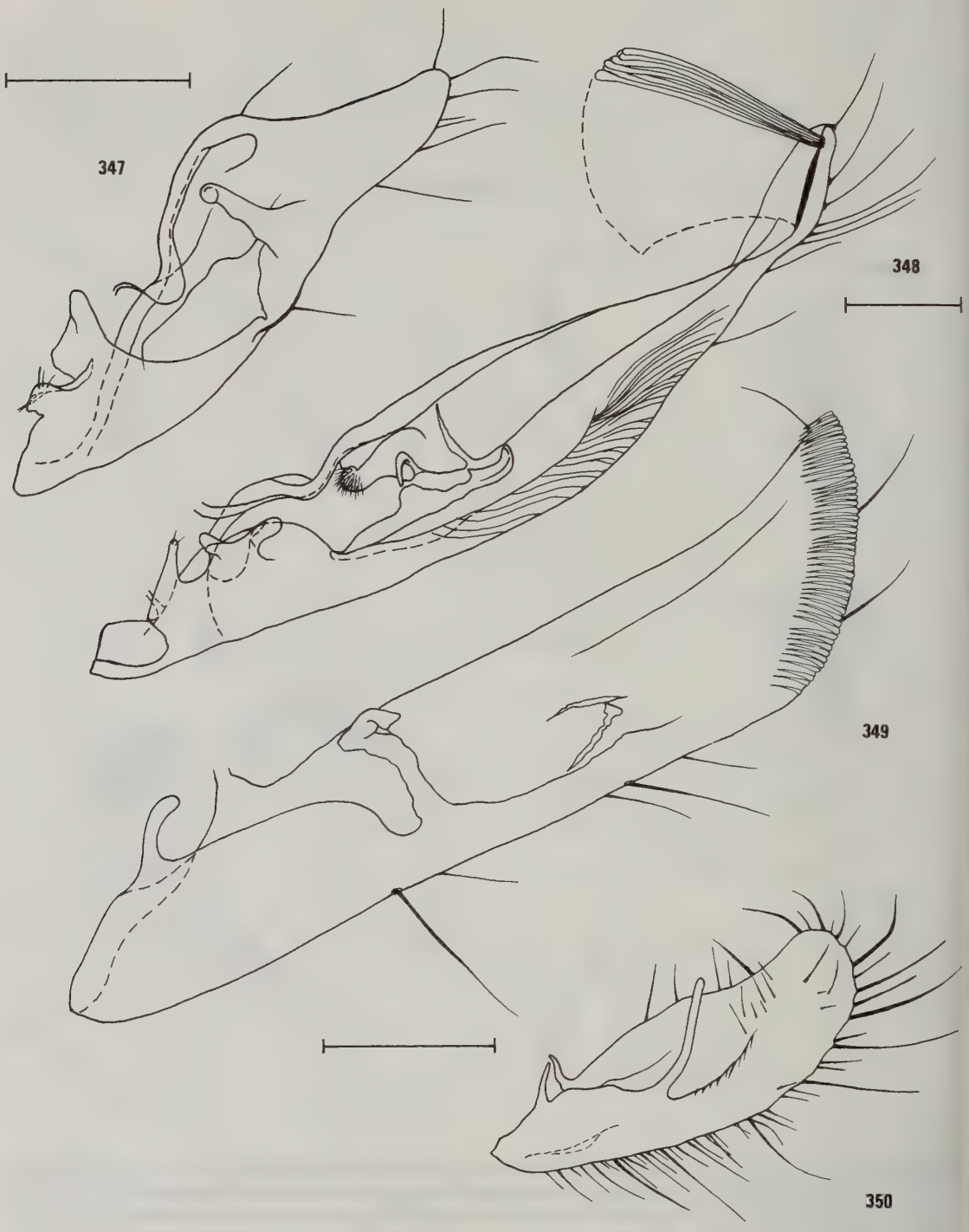
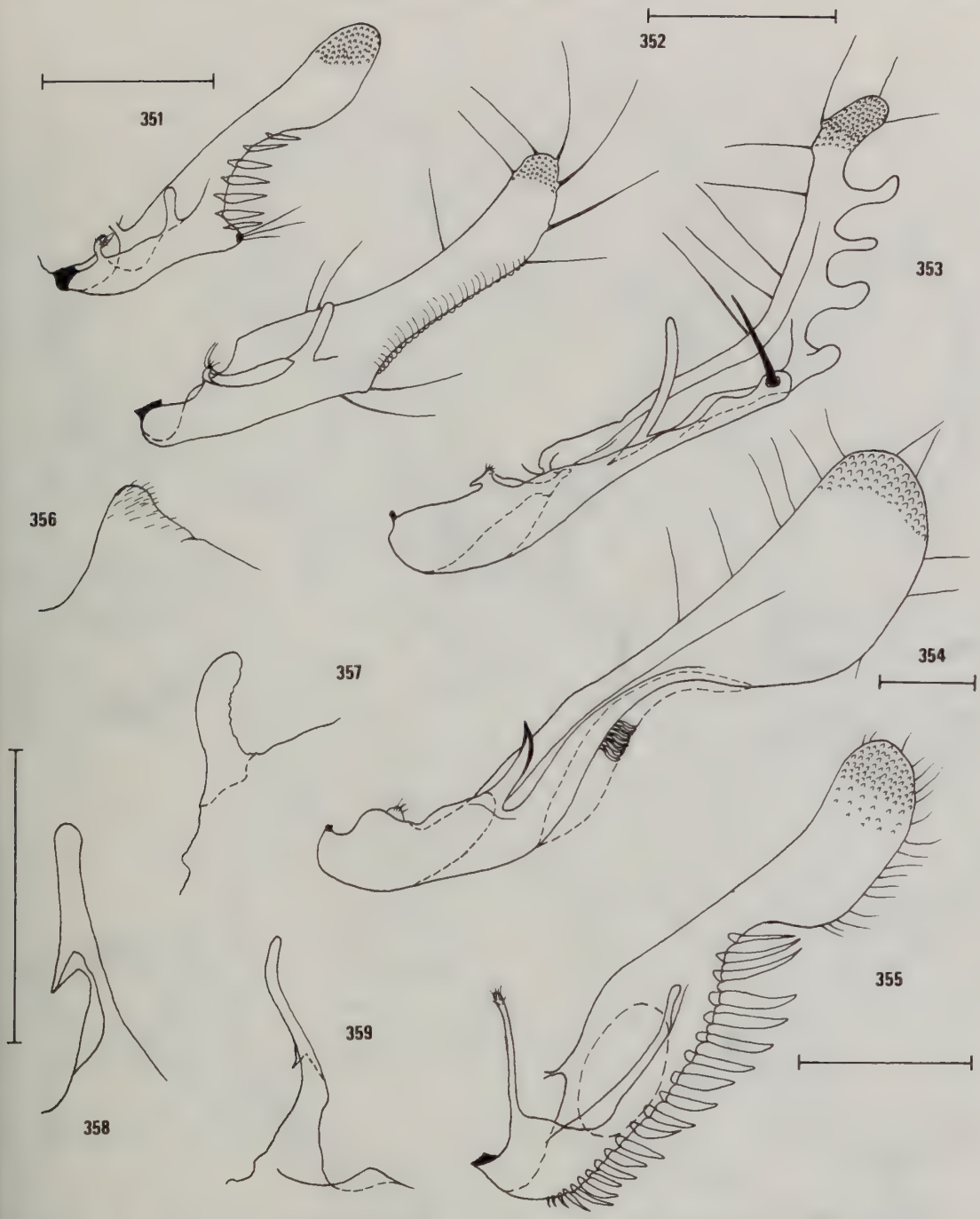


Figs 347–350 Left valves. 347, *Abrostola*. 348, *Mouralia*; note the apical twist to the valve, bearing a large fan of spatulate scales, the limits of which are indicated by the dashed line. 349, *Cucullia*. 350, *Polychrysia*.



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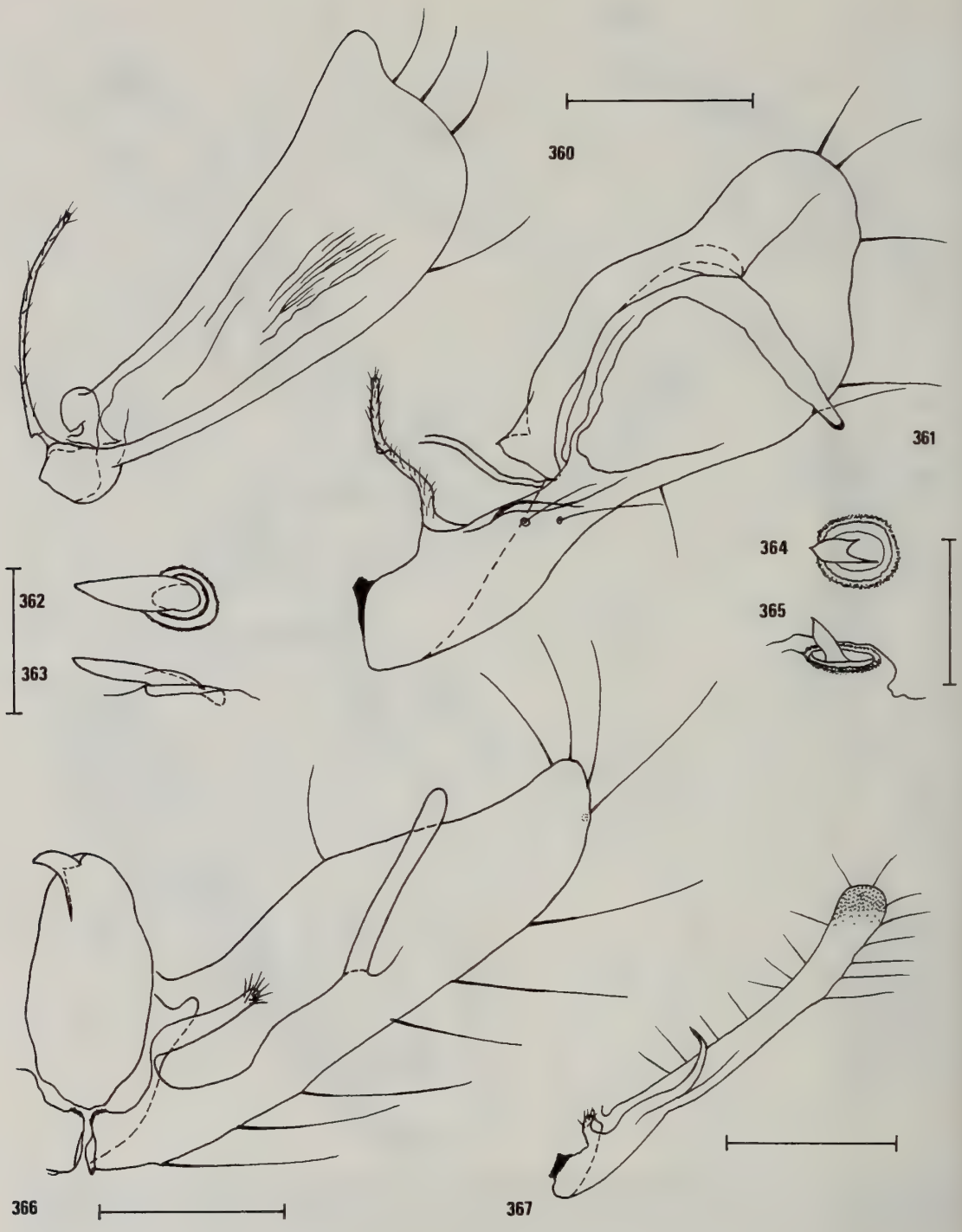

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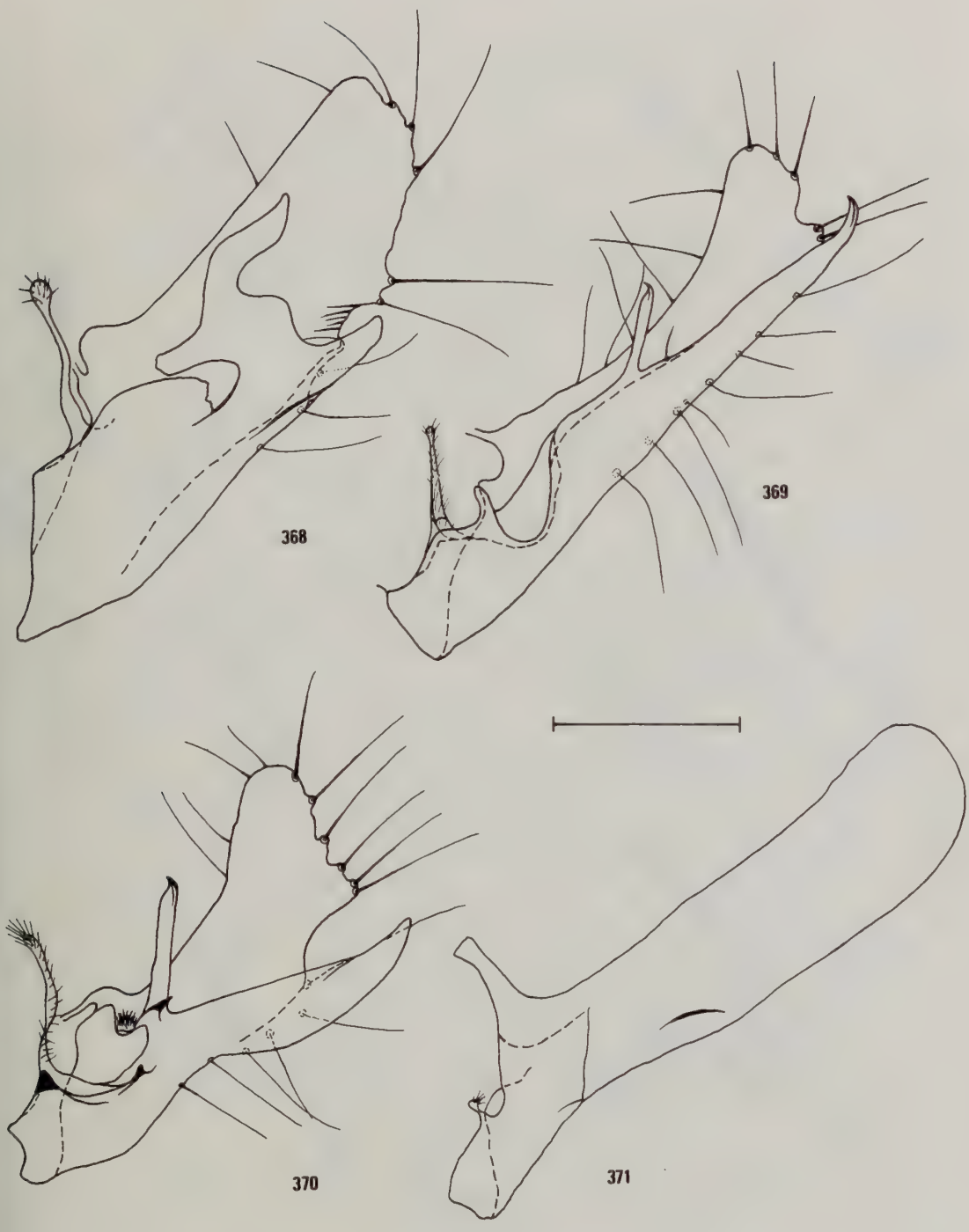

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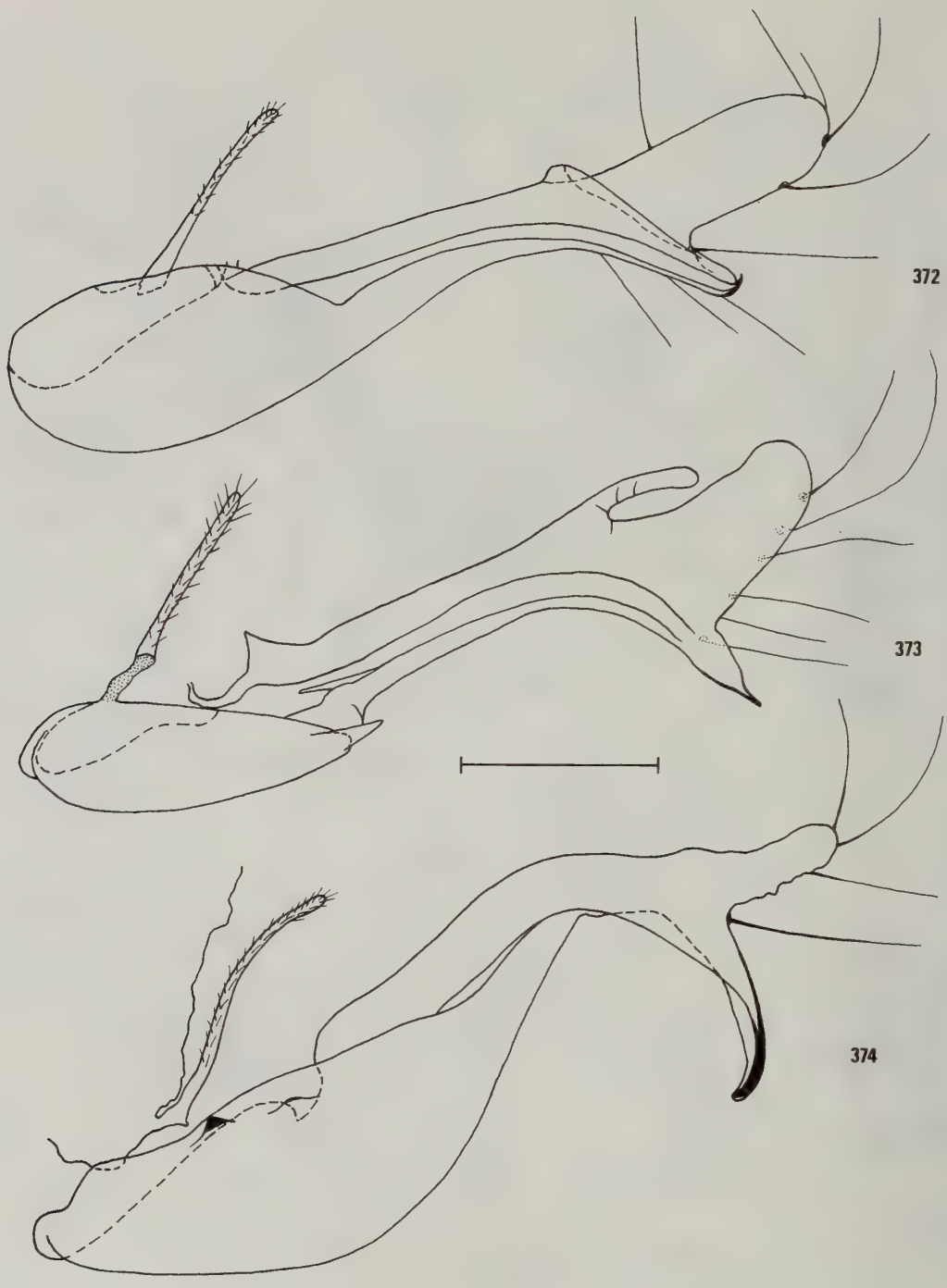

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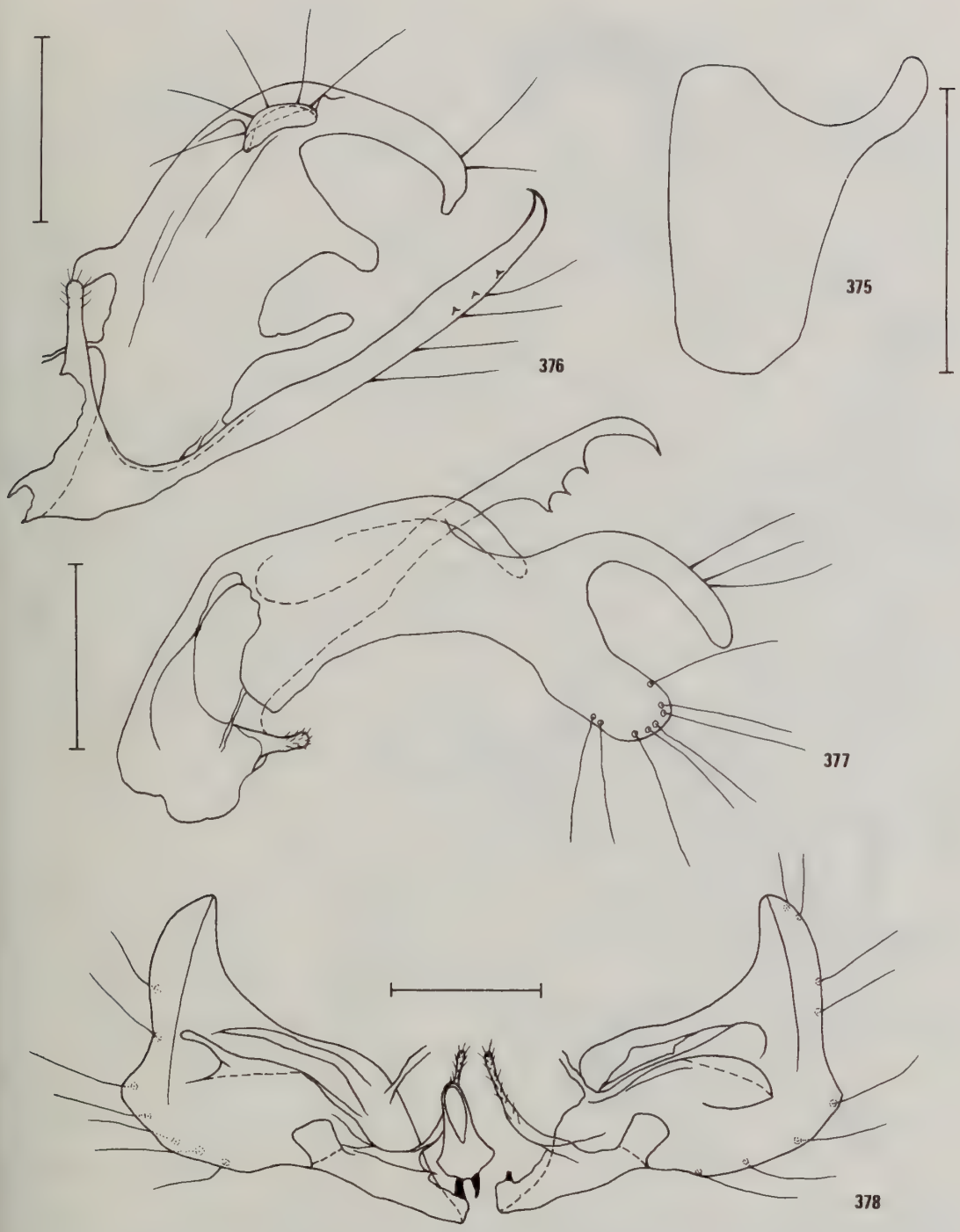

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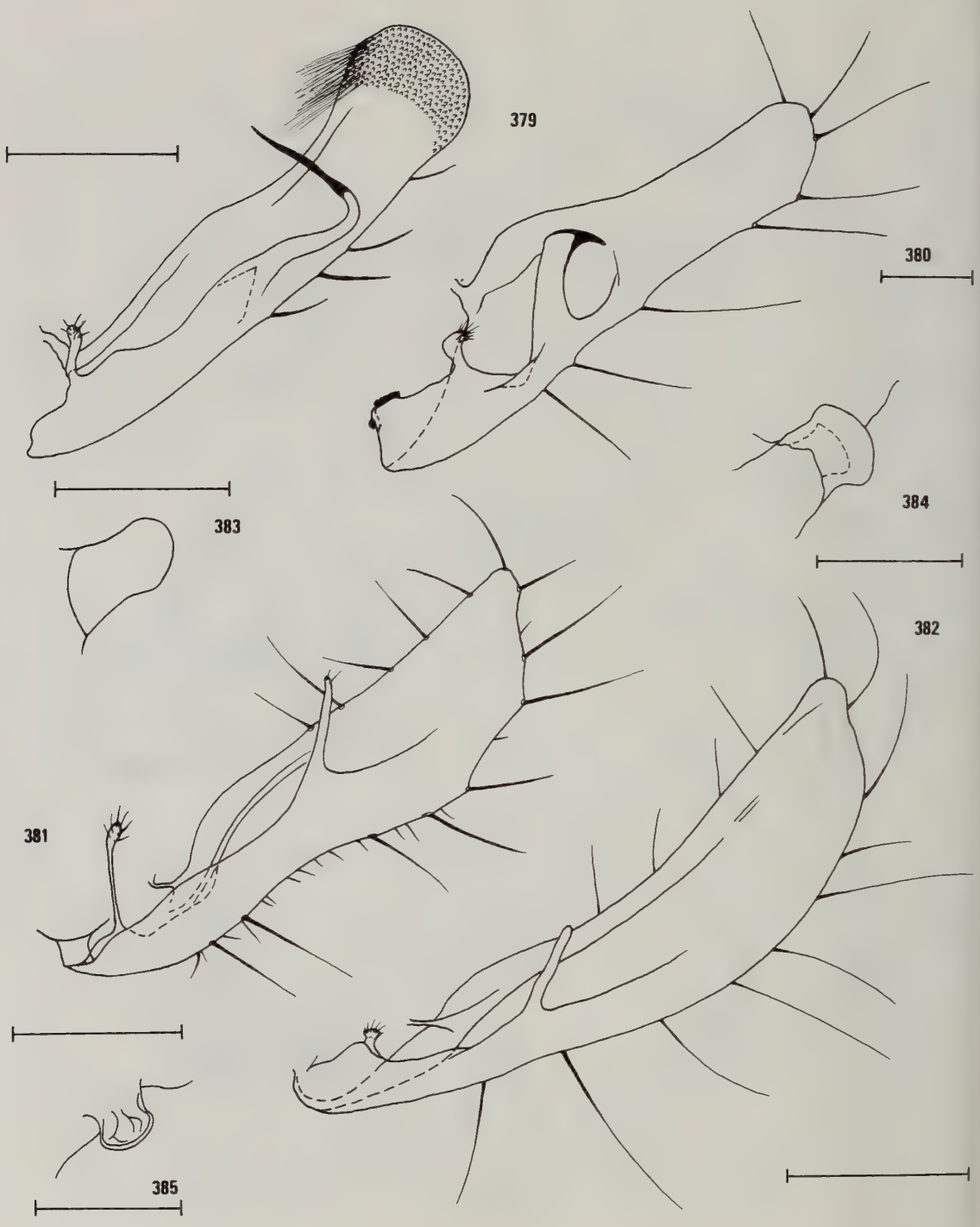

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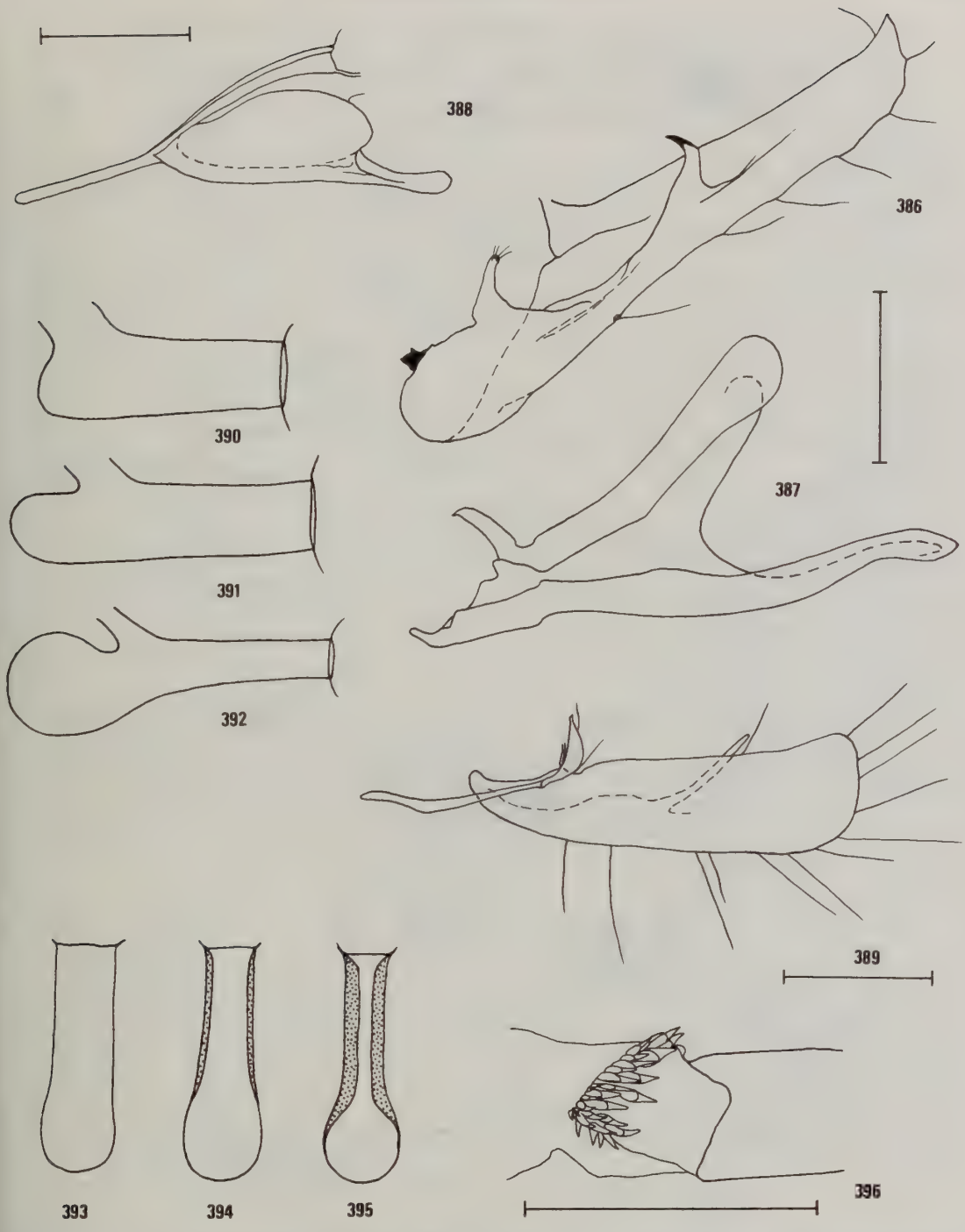

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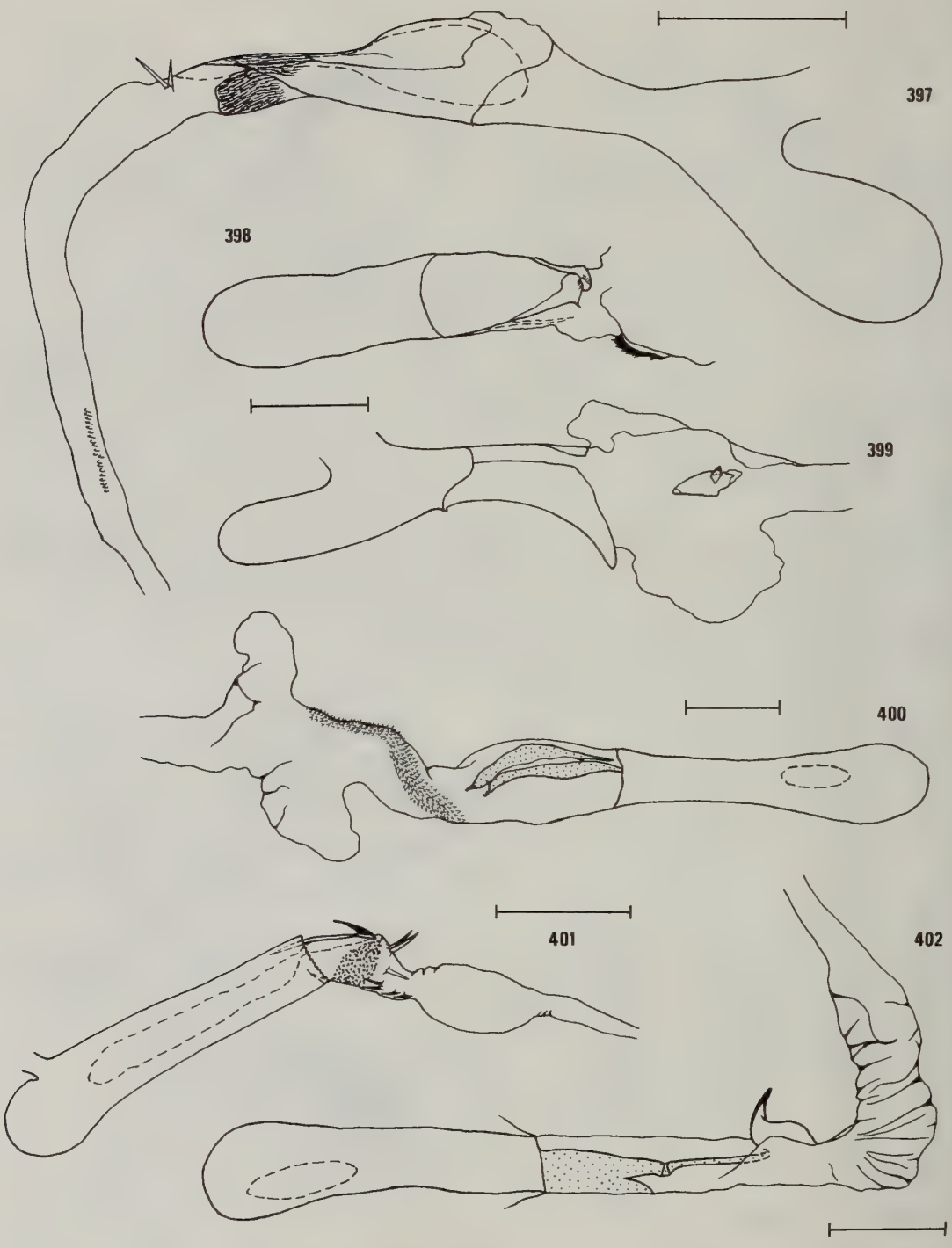

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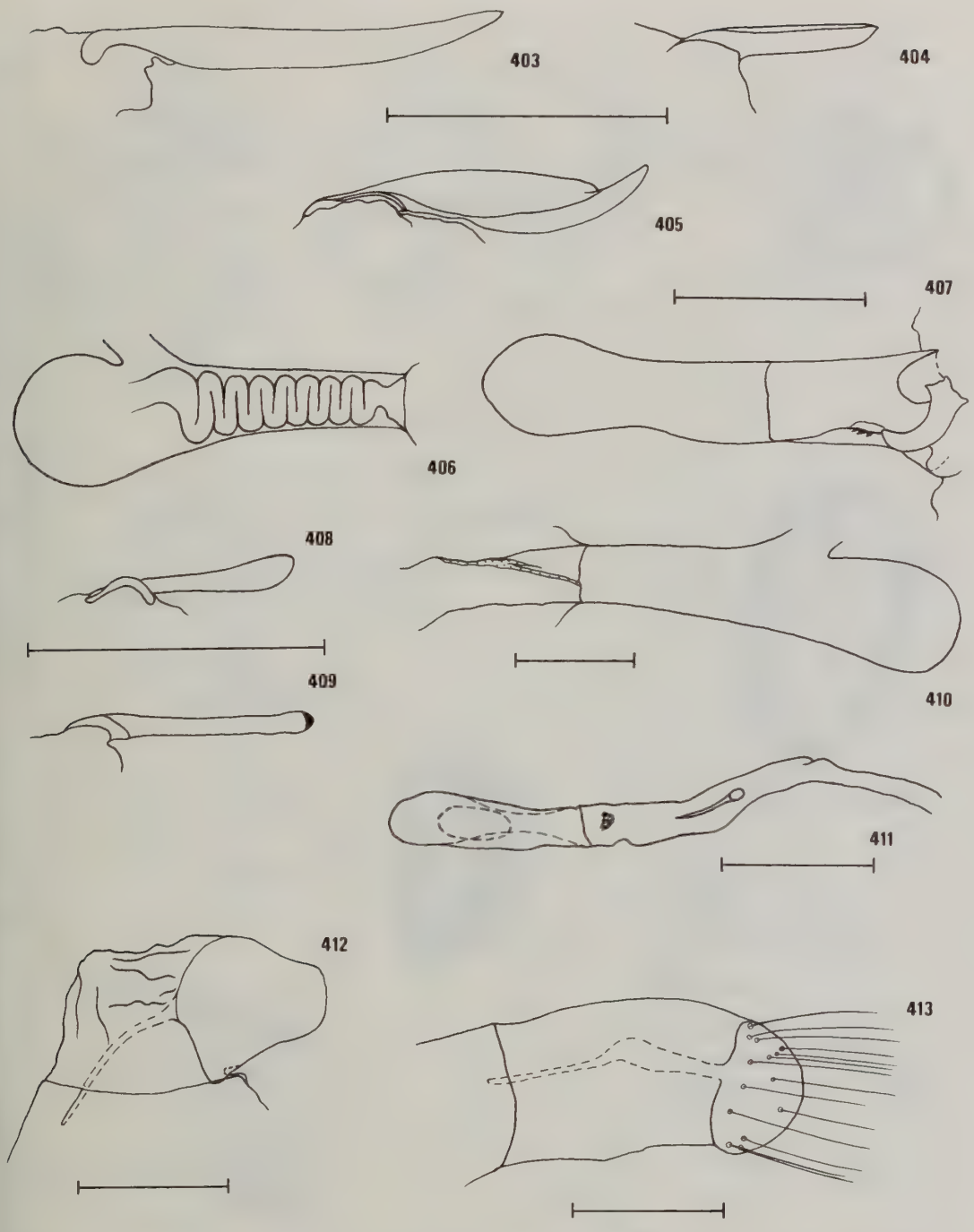

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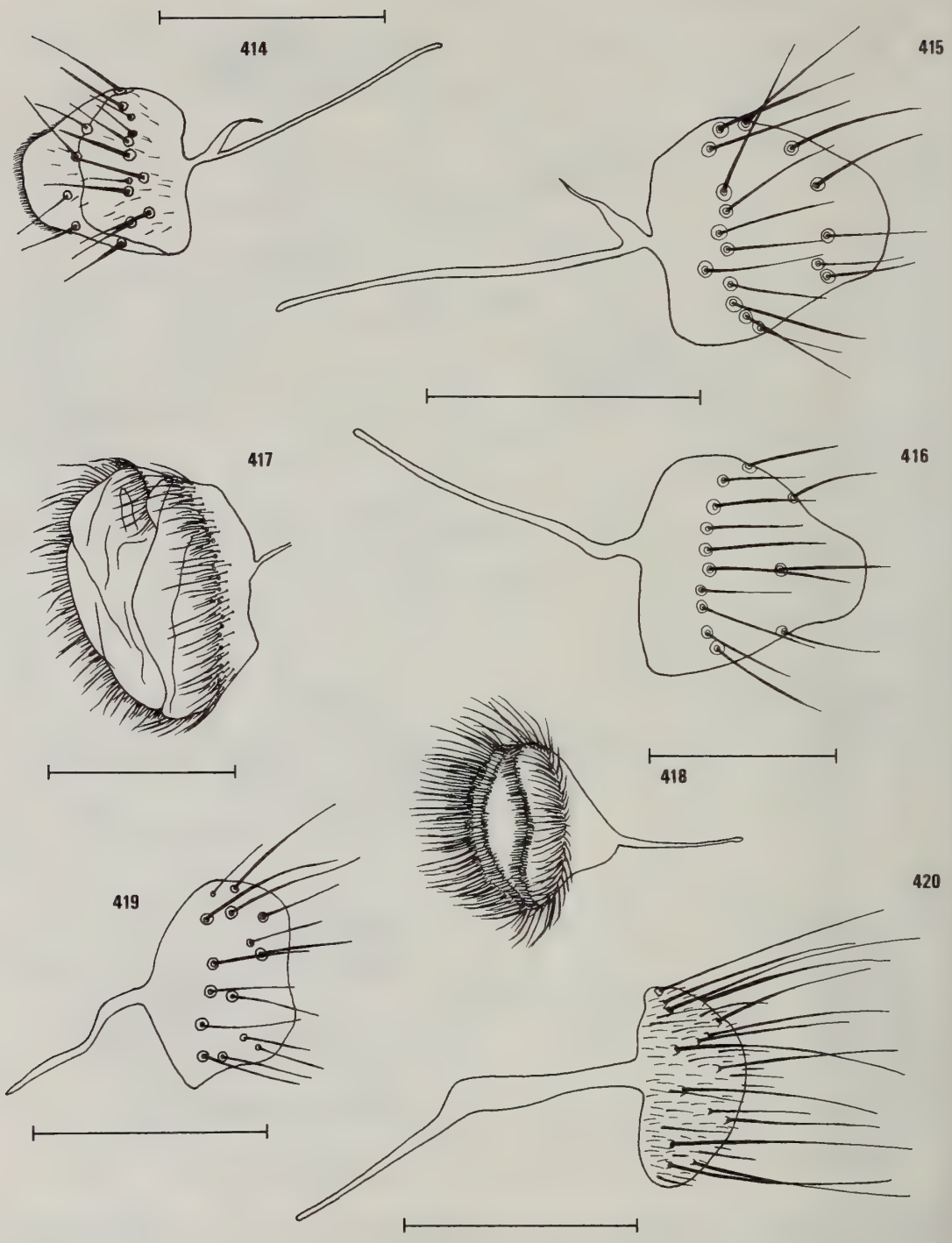

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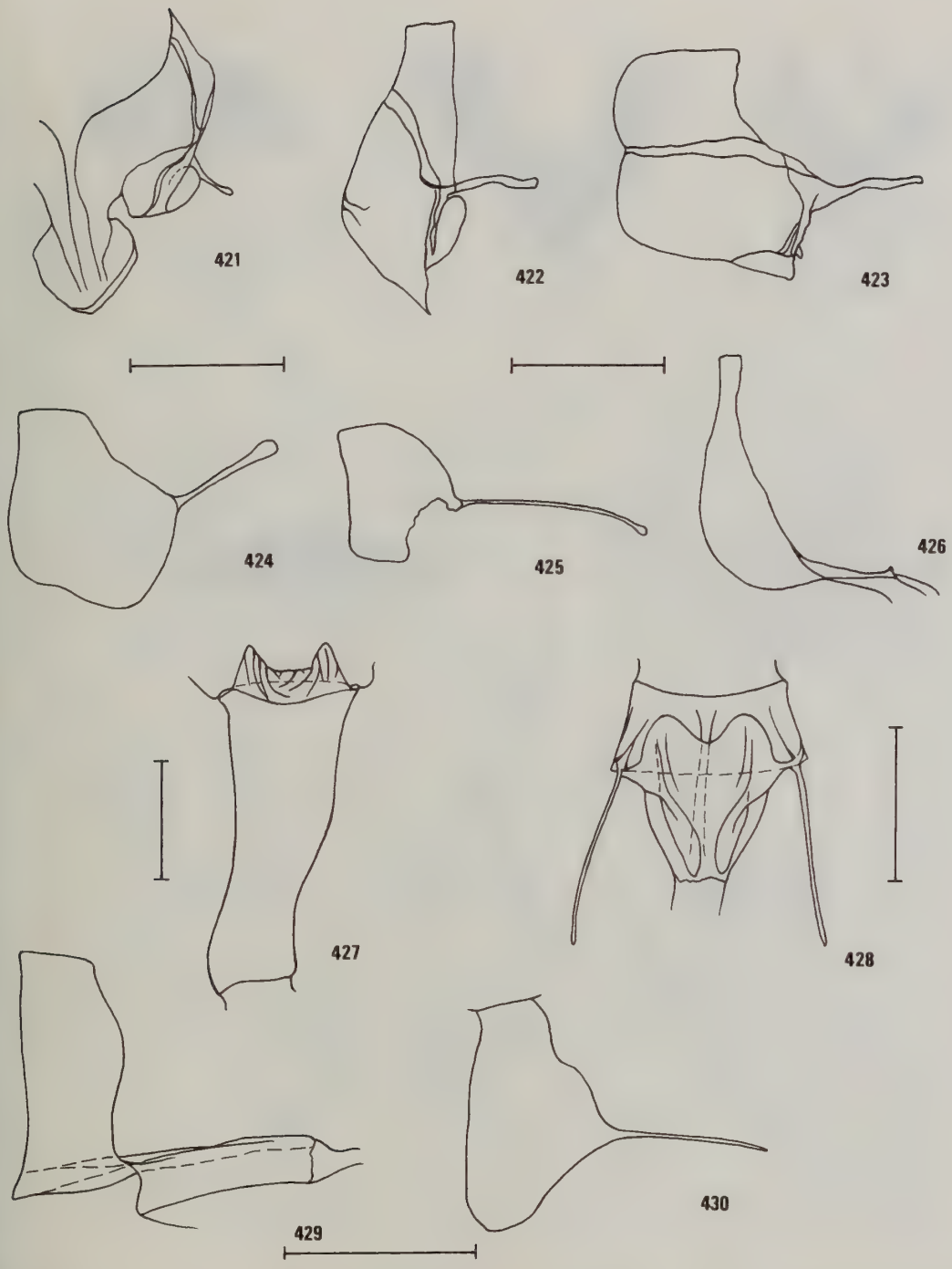

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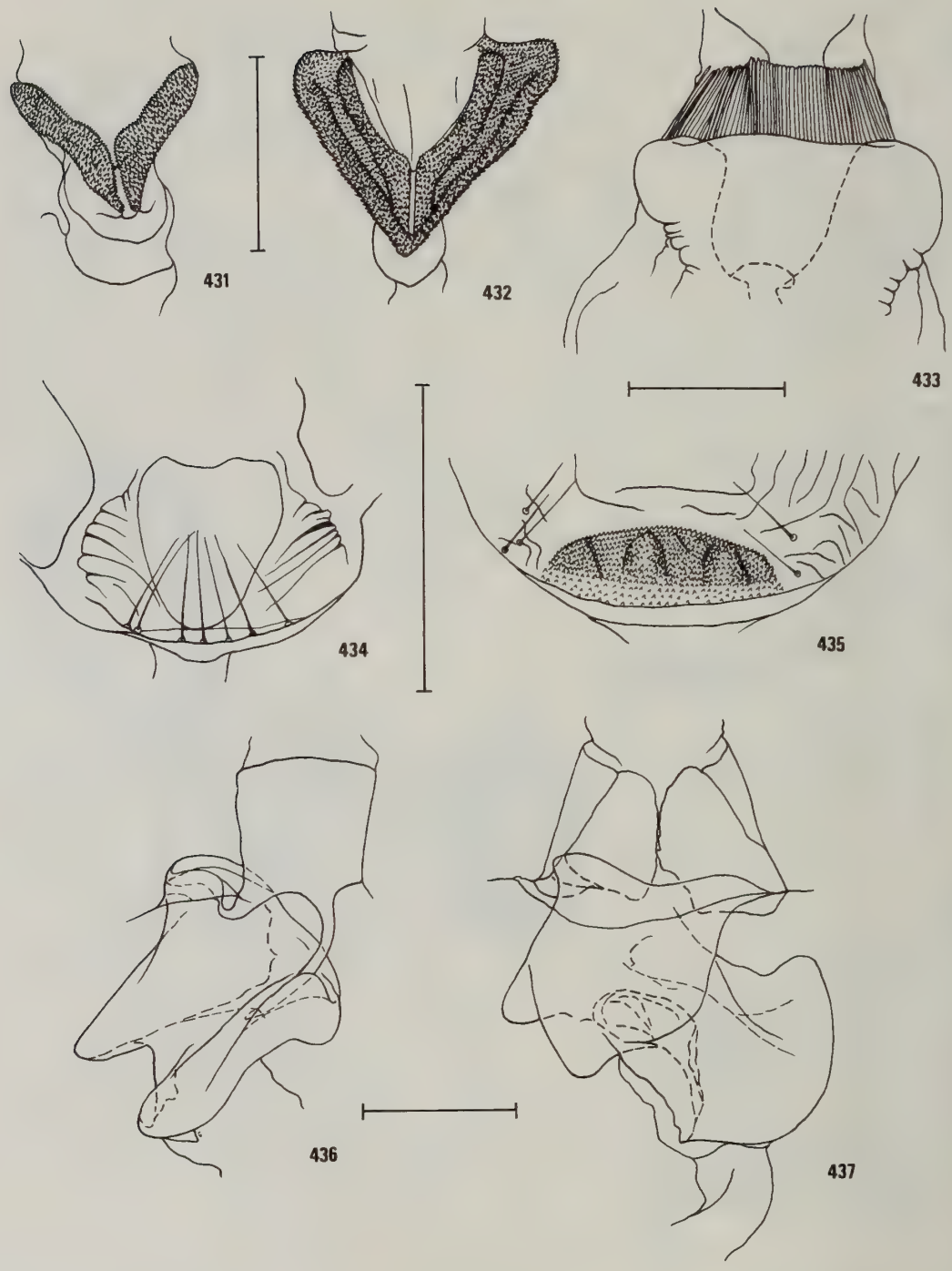

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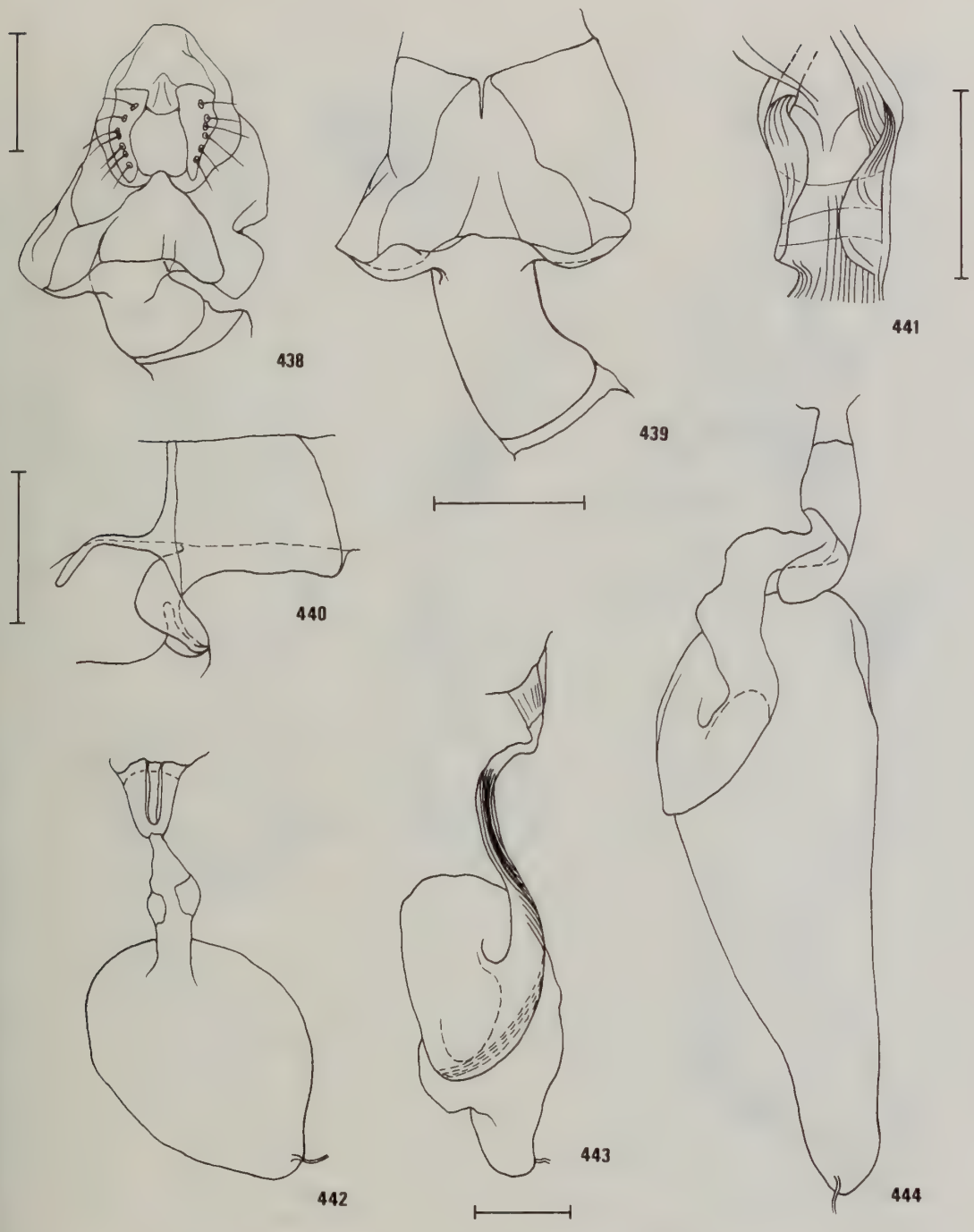

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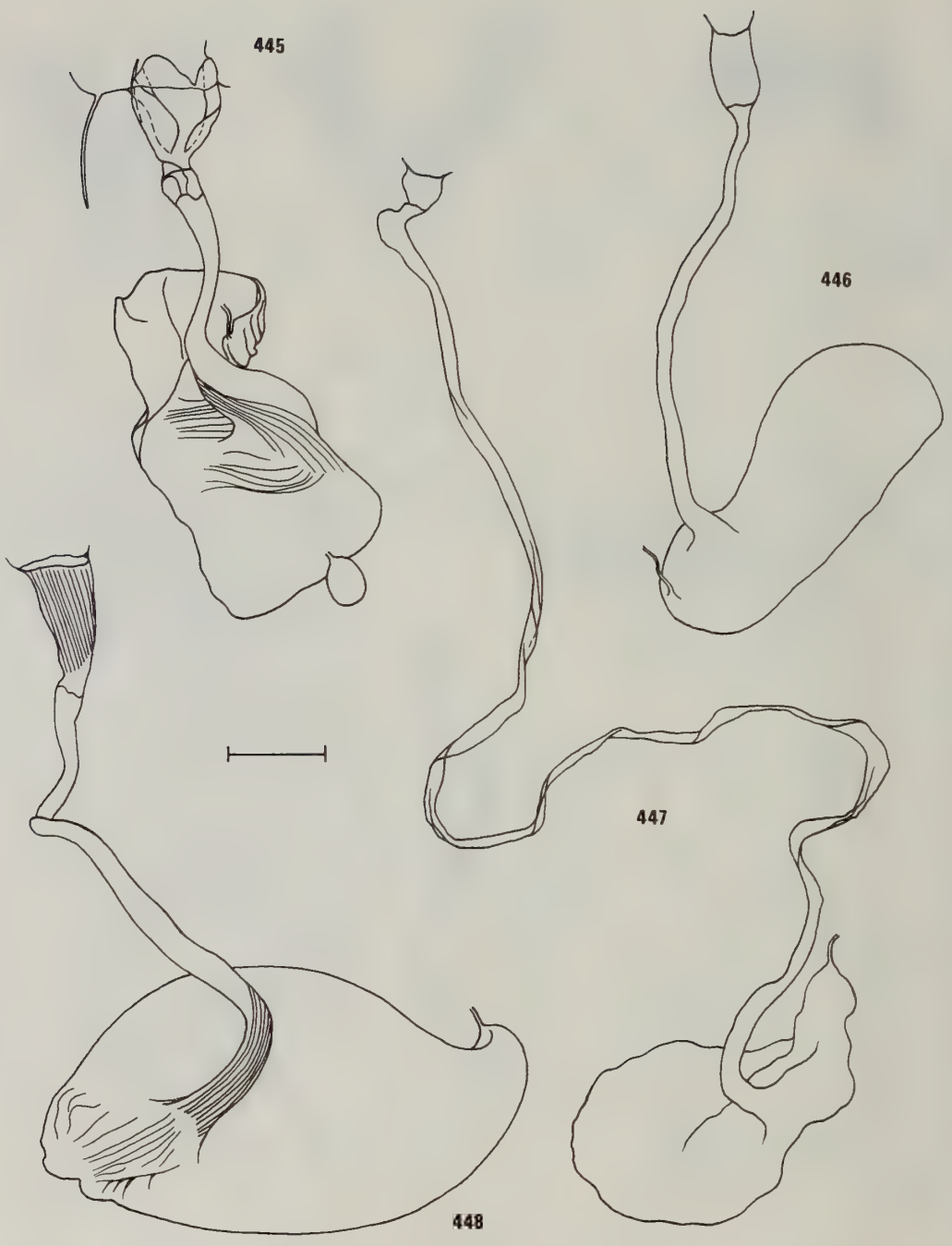

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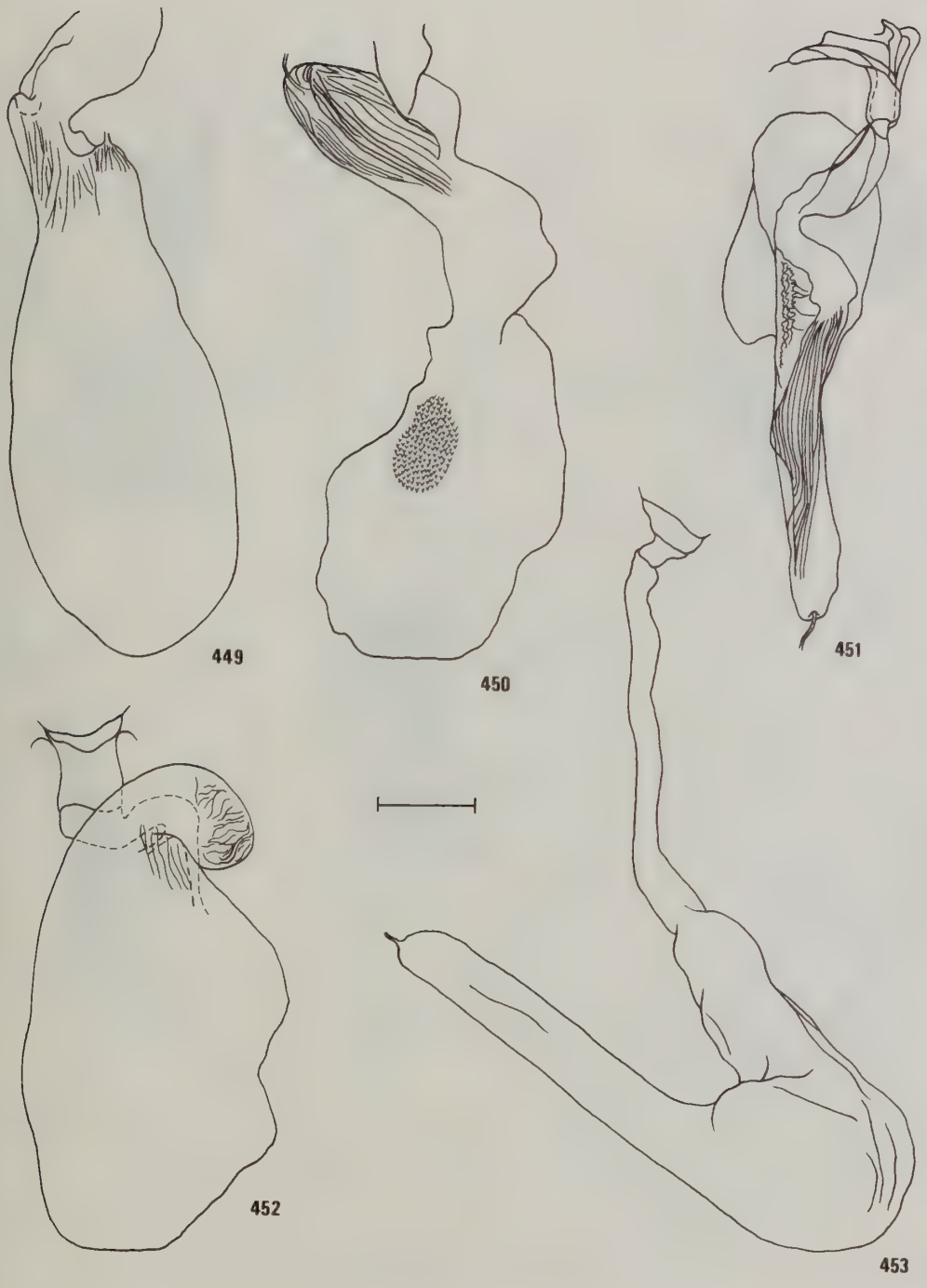

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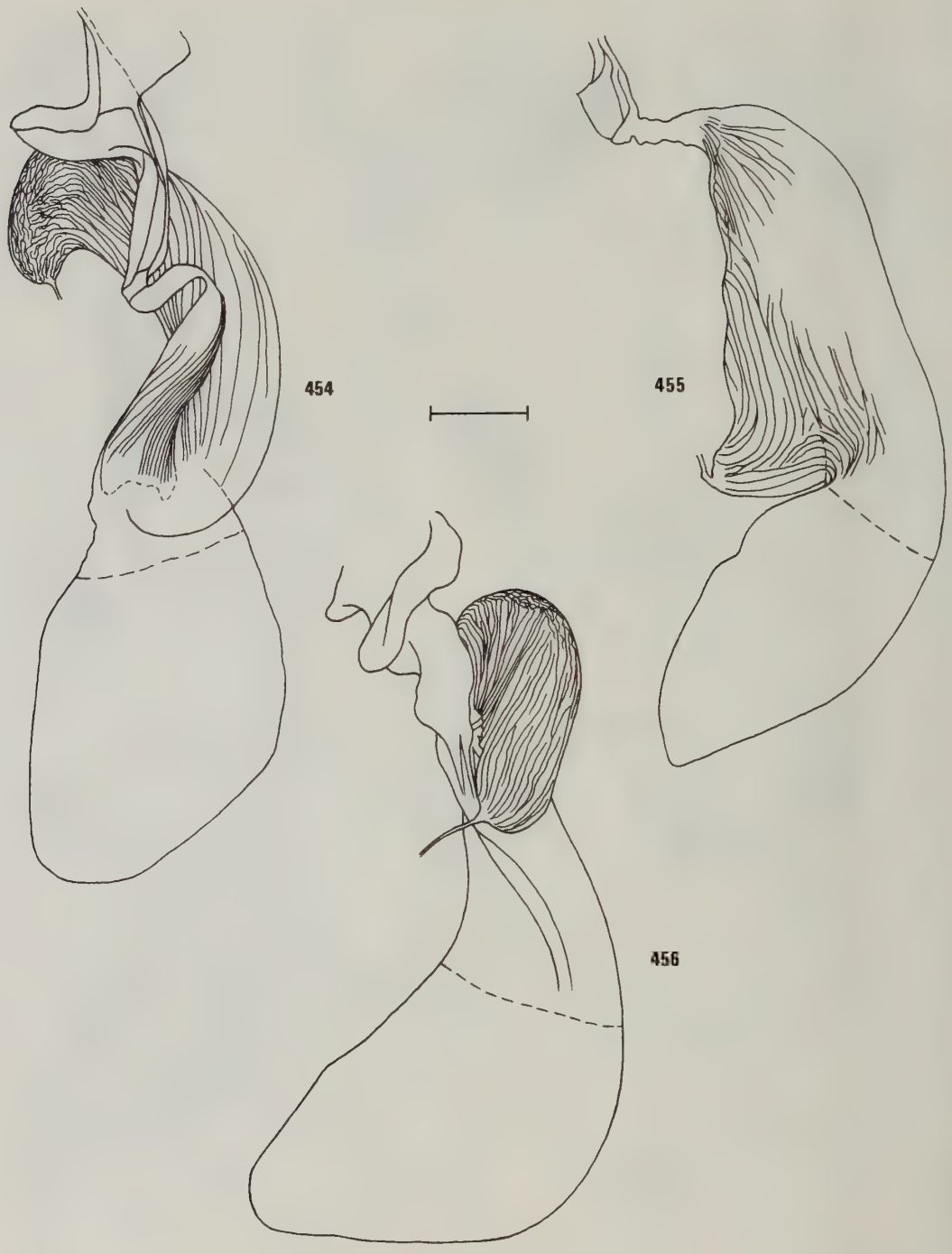

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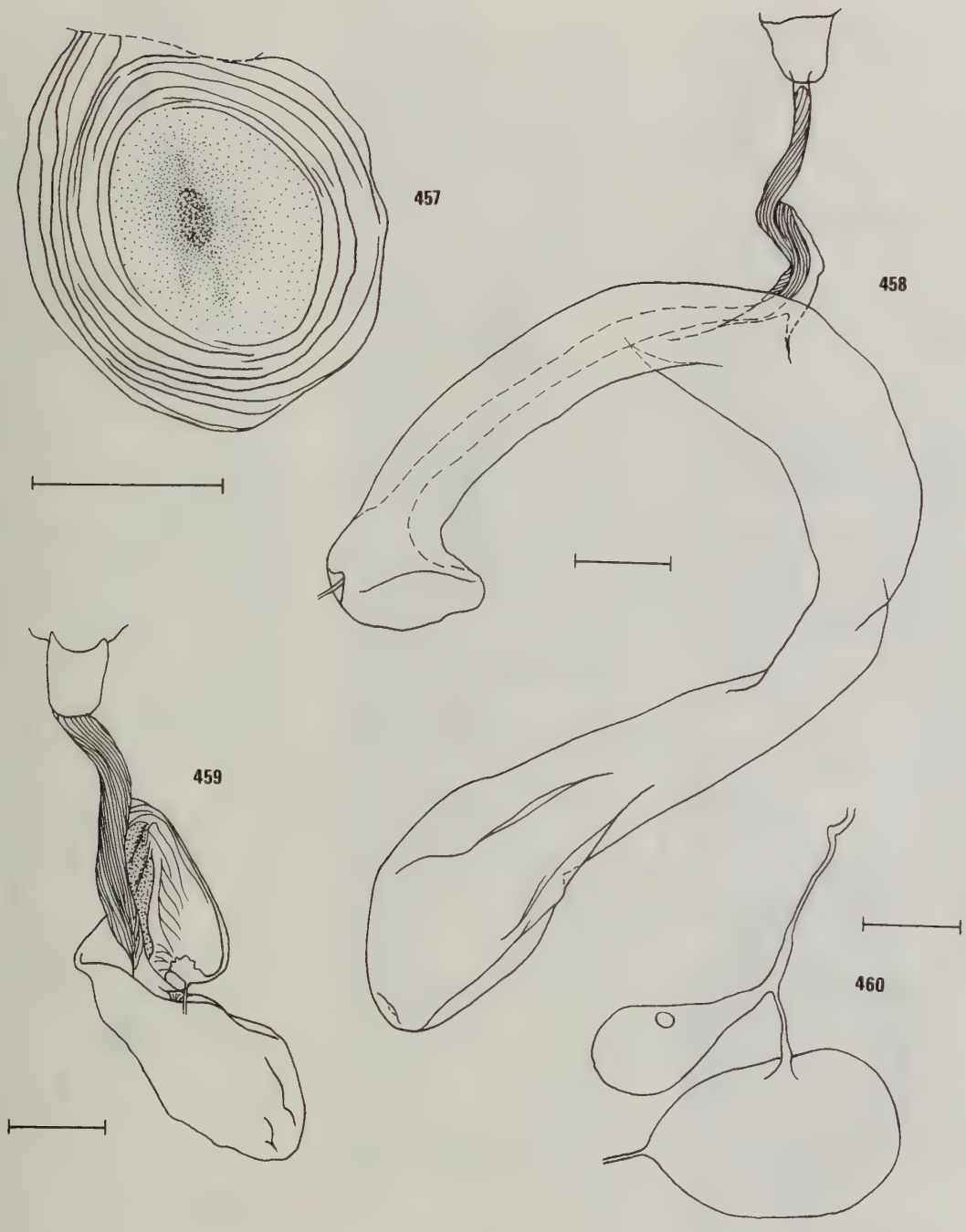

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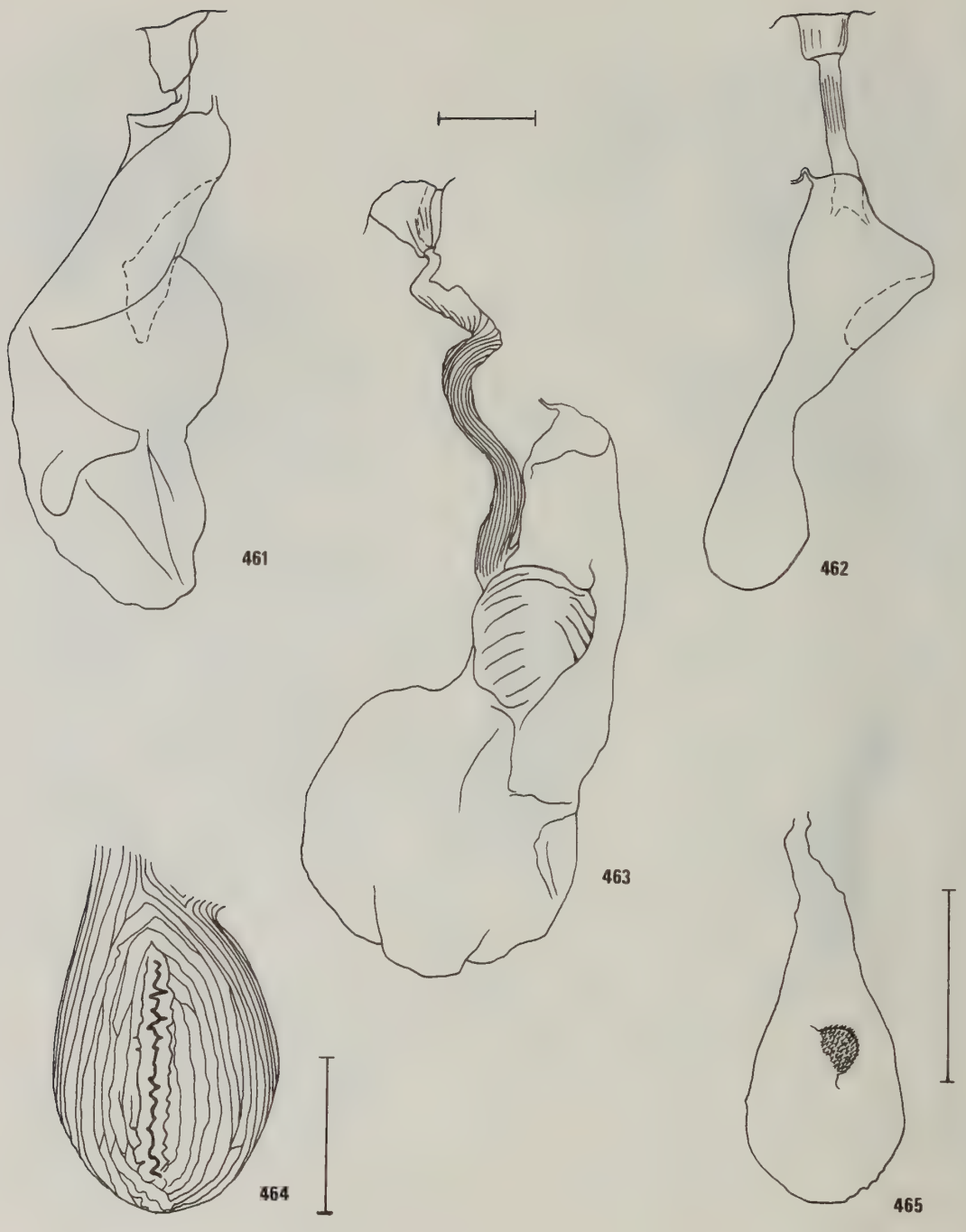

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P. R. Ackery & R. I. Vane-Wright

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